Ecophysiology

of Antarctic Lichens

by

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Abstract

The vegetation of the Windmill Islands oasis, Wilkes Land, continental Antarctica is dominated by lichens. Aspects of the ecology and physiology of lichens were studied during three summers and a winter period on the well vegetated Clark and Bailey Peninsulas in an attempt to explain patterns in lichen distribution. Most studies were done at a knoll on Clark Peninsula. This knoll has an extensive range of substratum nutrient levels and a variety of microhabitats, resulting in a variety of niches in a small area. At this site 29 identifiable species of lichen occur in seven sociations, most dominated in varying degrees by the macrolichens *Pseudephebe minuscula, Umbilicaria decussata, Usnea sphacelata* and *Usnea antarctica.* The crustose lichen *Buellia frigida* dominates sites on exposed boulders and a separate suite of species inhabits dead and dying moss. There are a suite of species which are restricted to sites with high nutrient levels, although the distribution of the dominant species is relatively insensitive to substratum nutrition. Exposure limits all species to various extents, with all lichens being intolerant of late-lying snow.

The nitrogen and phosphate content of lichen thalli is clearly related to that of the substratum on which they are growing. Monthly sampling of *Usnea sphacelata* and *Umbilicaria decussata* from eight sites identified a consistent trend in thallus nitrogen content with %N increasing throughout the winter and then dropping sharply with the onset of the melt and increasing during the summer. Lichen integrity during the middle of winter and before and after an unusual winter event were assessed by investigating the distribution of mineral nutrients within the lichen thallus. Although the distribution of minerals in the thalli differed between species and sites there was no effect of month and therefore the unseasonal rewetting and subsequent refreezing had little effect on membrane integrity.

The most important time for lichen photosynthetic activity was early summer from late October to early December. The increasing temperatures and insolation at this time lead to a great deal of snow melt and hence an increase in the availability of free water. Humidity was therefore high so that activation of photosynthesis was possible

through water vapour uptake alone. During the bulk of the summer lichens are photosynthetically inactive. At this time the air is too dry for lichens to absorb sufficient water from the atmosphere to initiate photosynthesis and hence they rely on direct moistening from summer snow falls and run off. The photosynthesis of the major species as a function of thallus water content was related to their observed distribution patterns.

Together, substratum nutrient levels, microclimate and photosynthetic characteristics of species can describe a great deal of the observed distribution patterns of lichens in the Windmill Islands.

Abbreviations used in thesis

ETR, apparent photosynthetic electron transport rate

F_o, minimum fluorescence with all PSII traps open in dark adapted chloroplasts

F_m, maximal fluorescence with all PSII traps closed in dark adapted leaves

F_t, fluorescence at time t

F_v, variable fluorescence

F'_m, maximal fluorescence in light adapted leaves

$\Delta F = F'_m - F_t$

LHCII, light harvesting chlorophyll *a*/*b* protein complex associated with PSII

IRGA, infrared gas analysis

PAR, photosynthetically active radiation

PPFD, photosynthetic photon flux density

PSII, photosystem II

q_P, coefficient for photochemical quenching of fluorescence

q_N, coefficient for non-photochemical quenching of fluorescence

ϕ_{PSII}, photochemical quantum yield of photosystem II

RH, relative humidity

Socn., sociation

WC, thallus water content.

Acknowledgements

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I also must thank all the members of the ANARE expeditions to Casey throughout 1991-1994 who supported the science program, especially all the 1992 winterers.

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Chapter 1

Terrestrial Antarctic Botany

1.1 Antarctica and terrestrial plants

Antarctica is the earth's highest, driest, coldest continent. The continent is divided into two bioclimatic zones; maritime Antarctica and continental Antarctica. Longton (1988) regarded the Maritime regions as cold-polar, the same as high Arctic regions, whilst continental Antarctica is described as frigid on the basis of its low maximum temperatures and extreme aridity (Figure 1.1). The frigid-Antarctic environment presents the most severe climate for terrestrial life on earth.

Since 98% of Antarctica lies under an ice sheet up to 5 km thick, terrestrial vegetation is restricted to the rugged coastal fringes, nunataks and inland mountain ranges and valleys which are occasionally to permanently ice-free. Such habitats are usually small, scattered and often isolated. Those few large ice-free regions, such as the dry valleys of Victoria Land, experience virtually no precipitation and are thus almost devoid of vegetation. Antarctica as a whole contains only approximately 80 bryophyte, 250 lichen and 2 angiosperm species (Smith 1984). Maritime Antarctica is the region with the greatest abundance and diversity of plant life including the two vascular plant species. Vegetation of the ice-free areas of continental Antarctica is restricted to bryophytes, lichens, algae and cyanobacteria, the total species number is low and vast areas are totally devoid of vegetation. As Walton (1984) pointed out, the critical biological factor in the ice-free regions is the presence of free water for at least part of the year, therefore the coastal areas which are normally snow covered in winter yet free of snow for some time in the summer are extremely important as habitats for terrestrial vegetation. Lichens dominate the vegetated areas of continental Antarctica and are able to withstand long periods of desiccation. Bryophytes are mostly restricted to areas with intermittent free water such as in drainage channels, the lee of semipermanent snow banks and around melt lakes. Terrestrial macroalgae are restricted to areas which remain moist for relatively extended periods.

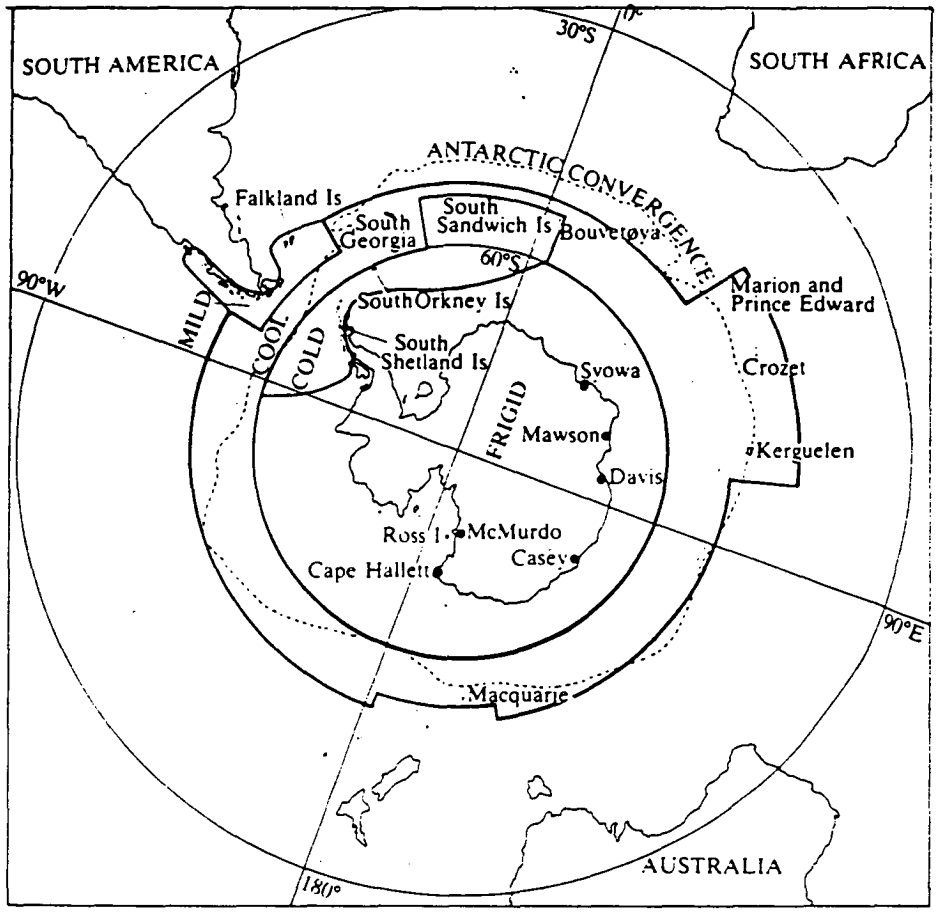

Figure 1.1 Map of Antarctica showing the position of the continent in relation to the other southern hemisphere land masses and the four climatic regions of mild, cool, cold and frigid. The cold and frigid regions are basically analogous to the maritime and continental bioclimatic divisions. From Longton (1988).

1.2 The Windmill Islands

This thesis is a study of the ecophysiology of lichens in the Windmill Islands oasis in Wilkes Land, continental Antarctica. The Windmill Islands cover an area some 40x15km on the eastern shore of Vincennes Bay (Figure 1.2) and consist of a series of low rounded islands and peninsulas. To the east of the exposed areas is a terminal moraine (Løken moraine) which marks the edge of the ice sheet of greater Antarctica. The maximum elevation of the exposed hillsides is 109m and the valleys in between are filled with snow and ice or glacial moraine. The geology of the area is relatively simple, being dominated by metamorphic schists, gneisses and migmatites with intrusion by Ardery Charnockite and Ford Granite in the south of the region (Figure 1.2). The area is currently deglaciating and there is sedimentological evidence that the southern igneous regions were exposed c. 8000 years BP and the northern regions c. 5500 years BP (Goodwin 1993).

The climate of the region is extreme. Using vegetation types as an indicator of climate, Longton (1988) classified the polar regions into four zones: mild-, cool-, cold- and frigid-polar. This revised classification scheme is believed to be more meaningful than previous ones and correlates most closely with mean summer temperature. The climate of the Windmill Islands is frigid-Antarctic with mean air temperatures for the warmest and coldest months of 0.3 and -14.9°C respectively, with a range from -41 to 9.2°C (Australian Bureau of Meteorology Records). The region had previously been classified as a polar desert on the basis of the very low level of precipitation (mean annual snowfall 175mm rainfall equivalent). Free water is scarce in most localities in continental Antarctica and is only present intermittently for short periods. Free water is available in early summer at times of snow melt and from snow showers through the summer. Very rarely sea fogs or mists provide water, but rain is almost totally absent. The region is subject to an average of 96 days of gale force winds each year with a maximum recorded gust of 146 knots (73 $m.s^{-1}$). Such winds come predominantly from the east.

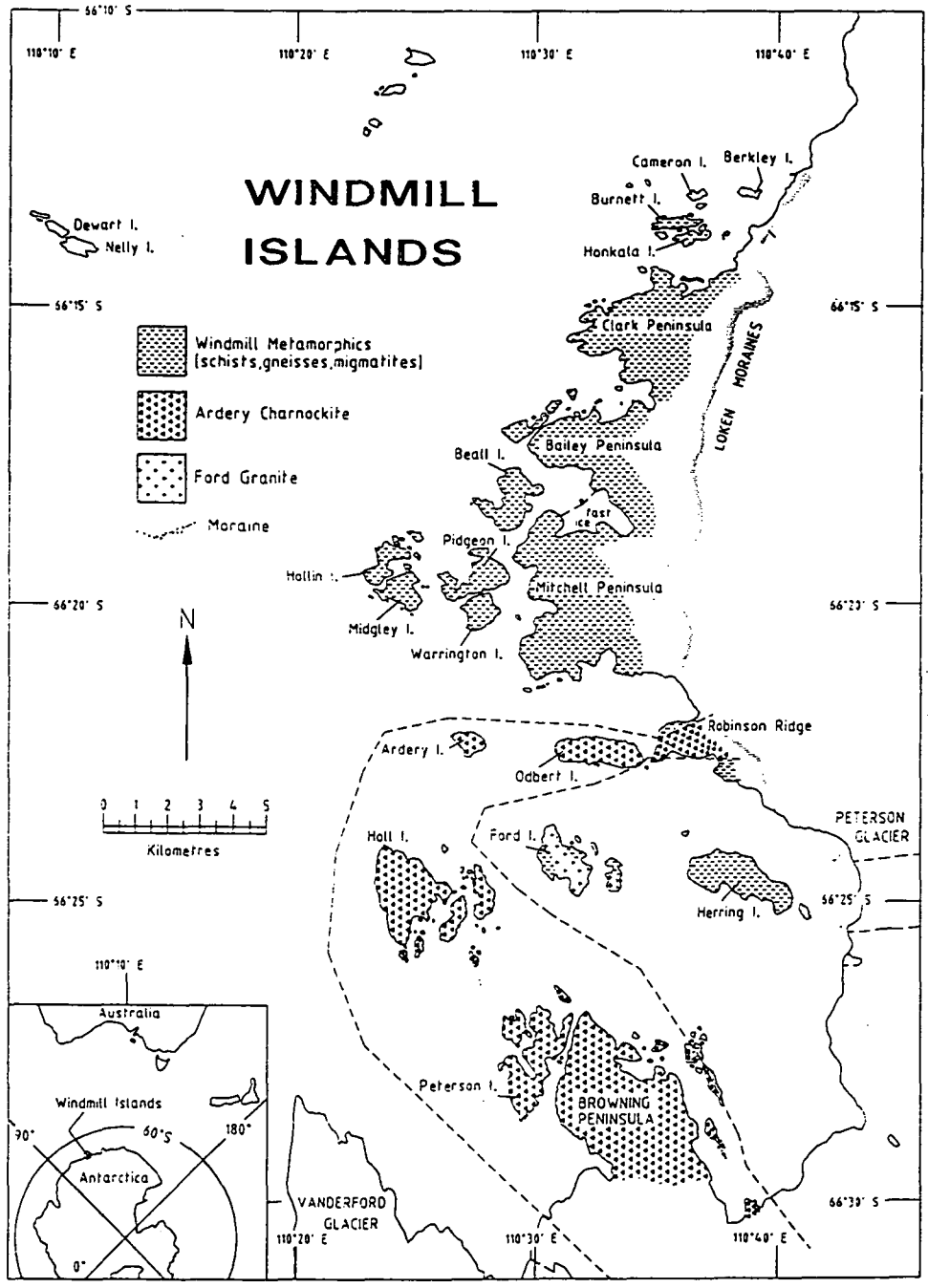

Figure 1.2 Map of the Windmill Islands showing the distribution of the major rock types after Blight and Oliver (1977). From Melick *et al.* (1994).

Due to the area's recent deglaciation coupled with the extreme climatic conditions, soil formation is limited. Silty soils and clays occur in areas of melt water accumulation and there is a very limited degree of podsolisation on the two northern-most peninsulas. Otherwise, soils are generally skeletal and formed of weathered chips of rock and gravel. There are numerous abandoned Adélie penguin (*Pygoscelis adeliae* Jacquinot et Hombron) rookeries throughout the Windmill Islands, situated generally at about 30m elevation. It is thought that as the land rose due to deglaciation these were abandoned in favour of sites closer to the water. There are, however, colonies presently occupied at higher elevations. Such abandoned rookeries consist of small, rounded pebbles from 5 to 15 cm in diameter, and occasional bleached penguin bones, feathers and egg shells. The soils in these sites are fine and silty, mostly derived from penguin guano, and are relatively rich in organic matter. The soils and gravels on Clark and Bailey Peninsulas are derived from Pleistocene marine sediments covered with more recently weathered rock.

1.3 Lichen biology

Biologists interested in studying lichens have long argued over an exact definition of a lichen. At the moment, the most widely accepted definition is that of Hawksworth (1994) which offers:

> "An ecologically obligate, stable mutualism between an exhabitant fungal partner (the mycobiont) and an inhabitant population of extracellularly located unicellular or filamentous algal or cynobacterial cells (the photobiont)."

The lichen thallus is relatively simple, with no roots and no cuticle, so metabolic activity is dependent upon direct moistening of the thallus (through rain, snow or run-off) or water uptake from a humid atmosphere. In many lichens the rate of water loss is rapid. Lichens exhibit a range of growth forms which may be classified into three main groups, crustose, foliose and fruticose (Hale 1983, Longton 1988). Crustose lichens are those in which the thallus lacks a lower cortex and is directly appressed to the substratum to immersed within it. This thesis classifies crustose lichens which occur exclusively on living or moribund moss as muscicolous. Foliose and fruticose lichens have a more or less aerial thallus which is either flattened and prostrate with one to several attachment points (foliose) or strap shaped to

shrubby, generally with a main axis (fruticose). Foliose lichens have an upper and lower cortex whereas fruticose lichens have an outer cortex.

Lichens dominate the terrestrial vegetation of continental Antarctica. This is mostly seen as being due to their ability to withstand long periods of desiccation and to regain metabolic activity almost immediately upon rewetting. There are no known cyanobacterial lichens in continental Antarctica and the green algal lichens have the ability to absorb moisture directly from humid air and can maintain a positive carbon balance at very low temperatures (Kappen 1989, Lange *et al.* 1989). In addition to this, Antarctic lichens are physically tough, being able to withstand desiccating winds and abrasion by ice and snow particles. One of the most remarkable features of Antarctic lichens is that they can withstand freezing even when fully hydrated (see Chapter 8).

The terrestrial vegetation of continental Antarctica is one of the simplest in terms of structure and the boundaries between community types are often sharp and definite. If we are to grasp the functioning of ecosystems effectively, a useful place to start is with a simple system with strong environmental determinants, yet with sufficient complexity to generate interesting and meaningful hypotheses. This study is an attempt to increase our understanding of the ecology and physiology of lichens from continental Antarctica, in particular what major factors govern the distribution and abundance of both restricted and widespread lichens, and how an understanding of the physiology of the dominant lichen species can assist our interpretation of ecological patterning and hence of ecosystem structure and function. In all this thesis will describe the vegetation of the Windmill Islands in general, the microclimatic conditions which lichens experience through the year in a well vegetated site, the photosynthetic attributes, water relations and nutrition of major lichen species and the influence of site conditions on the distribution of lichen communities. To do this, I spent three summers and one winter at Casey station investigating the lichens in both the field and laboratory.

Chapter 2

The vegetation of the Windmill Islands

2.1 General description of vegetation

The Windmill Islands is the site of the best developed and most extensive vegetation cover of any area in continental Antarctica. At least 29 species of lichens, five mosses and one liverwort have been identified there (Smith 1988a, Melick *et al.* 1994). The latest list of lichen and bryophyte species is given in Table 2.1, along with the growth form of each lichen species. In addition to the species listed, there are several lichens of unknown affinity and an undetermined number of species from the genus *Lecidea sensu lato.* There are also approximately 200 species of terrestrial algae and cyanobacteria and two forms of an "indeterminate crust" (Melick *et al.* 1994), which appears to be lichenized *Desmococcus olivaceus* (Pers. ex Arch.) Laundon. The nomenclature adopted in this thesis follows Castello (1995), Castello and Nimis (1994) and Seppelt *et al.* (1995).

The dominance of crustose lichens in the flora is characteristic of continental Antarctica (Longton 1988). As conditions become progressively harsher, lichen thalli become more appressed to the point where the lichens may become entirely endolithic in the most severe habitats (e.g. in sandstones in the dry valleys of Victoria land).

The local species richness declines from the north to the south in the Windmill Islands. The most species rich areas occur on Clark Peninsula, Bailey Peninsula and Robinson Ridge (Figure 2.1). Development of vegetation is also greatest on the northern peninsulas where extensive stands of lichens occur (Figure 2.2, Figure 2.3). The nearby coastal islands are only slightly vegetated by comparison, despite their similar geology, probably due to salt spray deposition. Two islands have quite high species diversity (Beall I. 12 spp. and Hollin I. 16 spp.), but the vegetation occurs in isolated microsites, never forming the extensive stands so obvious on the peninsulas. Vegetation is very restricted in the southern charnockitic areas, both in extent of development and in species richness. The most northern islands are vegetated only by algae due to the presence of large numbers of nesting penguins during the summer. These sites are very high in organic nutrients and are hypersaline (Melick *et al.* 1994).

TABLE 2.1 Bryophyte and lichen species list for the Windmill Islands with growth form for lichen species (c= crustose, e = endolithic, fo= foliose, fr= fruticose, m= muscicolous).

Acarospora gwynii Dodge et Rudolph	c
Pleopsidium chlorophanum (Wahlenb.) Zopf =*Biatorella cerebriformis* (Dodge) Filson	c
Buellia frigida (Darb.) Dodge	c
Buellia grimmiae Filson	m
Buellia latemarginata Darb.	c
Buellia lignoides Filson	c
Buellia papillata Tuck.	m
Buellia soredians Filson	c
Caloplaca athallina Darb.	m
Caloplaca citrina (Hoffm.) Th. Fr.	m
Candelariella flava Castello et Nimis = *Candelariella halettensis* (Murray) Øvst	m
Lecanora expectans Darb.	m
Lecidea cancriformis Dodge et Baker	e
Lecidea sp.	c/m
Lepraria	m
Physcia caesia (Hoffm.) Hampe.	fr
Pseudephebe minuscula (Nyl. ex Arnold) Brodo et Hawksw.	fr
Rhizocarpon flavum Dodge et Baker	c
Rhizoplaca melanophthalma (Ram.) Leuck. et Poelt	e
Rinodina olivaceobrunnea Dodge et Baker	m
Rinodina petermannii (Hue) Darb.	c
Umbilicaria aprina Nyl.	fo
Umbilicaria cristata Dodge et Baker	fo
Umbilicaria propagulifera (Ras.) Llano	fo
Umbilicaria decussata (Vill.) Zahlbr.	fo
Usnea antarctica DuRietz	fr
Usnea sphacelata R.Br.	fr
Xanthoria candelaria (L.) Th. Fr.	c
Xanthoria elegans (Link) Th. Fr.	fr

MOSSES

Grimmia antarctici Card.
Grimmia lawiana Willis
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer et Scherb.
Bryum argenteum Hedw.
Ceratodon purpureus (Hedw.) Brid.

LIVERWORT

Cephaloziella exiliflora (Tayl.) Douin

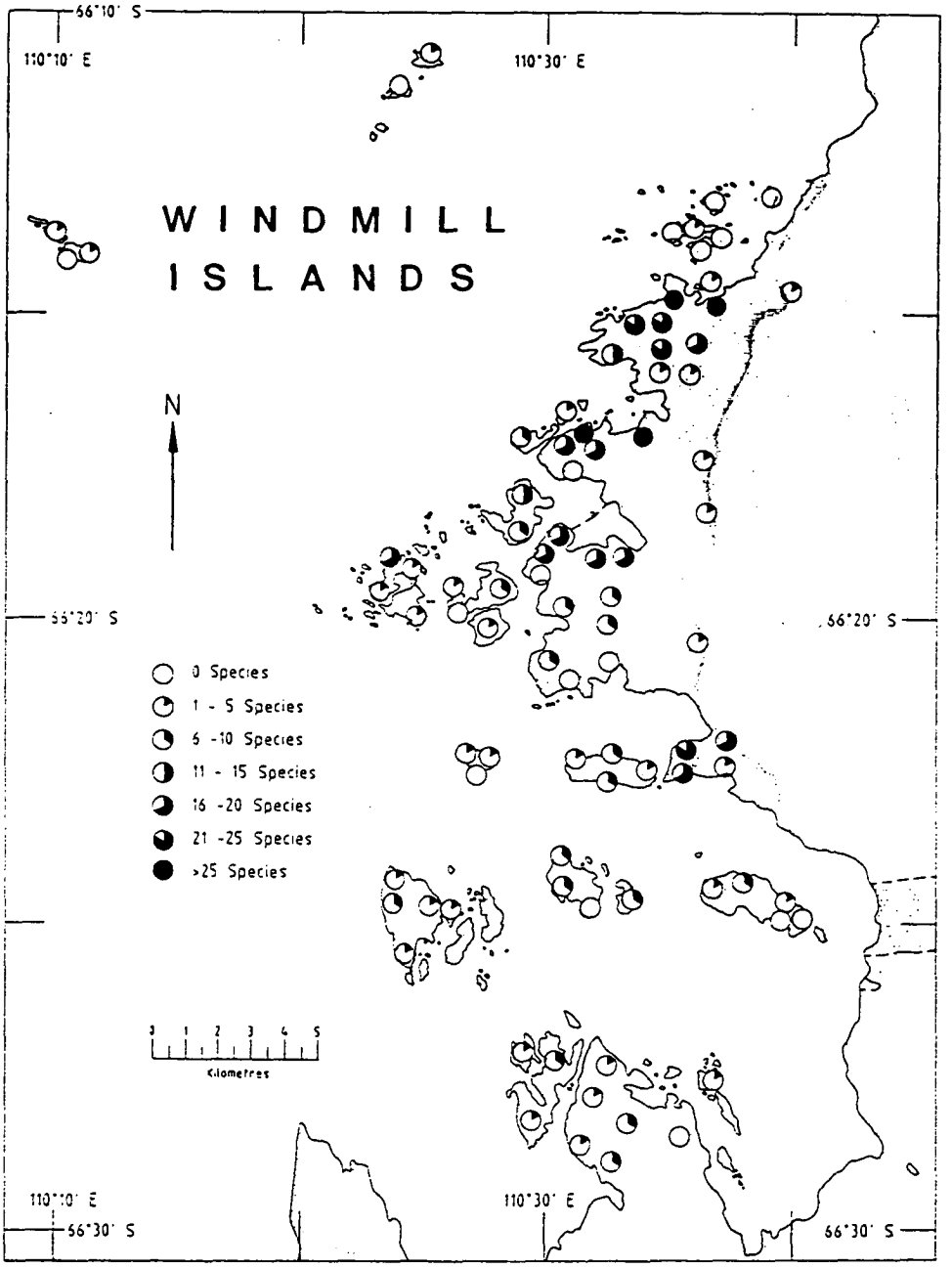

Figure 2.1 The number of bryophyte and lichen species recorded from sites throughout the Windmill Islands. From Melick *et al.* (1994).

The marked decline in vegetation frequency and species richness from north to south is undoubtedly linked with the nature of the dominant substrata. It is unlikely that the lack of vegetation is a chance event since the southern region was deglaciated before the northern region (Goodwin 1993) and the common north-easterly winds (see Figure 3.2) could deliver propagules from the well vegetated areas on the northern peninsulas. There is also very little difference in overall soil chemistry between the well vegetated northern and the poorly vegetated southern ends of the Windmill Islands (Melick *et al.* 1994). It seems most plausible to attribute the lack of vegetation to the differences in substratum structure between the igneous and metamorphic rocks. The schists and gneisses of the northern peninsulas and islands typically have a stable, finely crystalline structure and tend to wear smoothly, whereas the coarse grained charnockite and granite are prone to deep physical and chemical weathering and intricately shaped, wind-eroded rocks are common in the southern regions. Herring Island seems to be particularly susceptible to weathering, with whole boulder faces exfoliating at a touch. It is easy to see that a slow growing propagule would find difficulty establishing on such a temporary subtratum.

On a smaller scale, the vegetation on the most richly vegetated peninsulas and islands is best developed on the northern aspects. This is particularly evident on Mitchell Peninsula where, despite similar substratum structure and chemistry, the vegetation varies from well developed stands with 17 species in the north to large outcrops totally devoid of vegetation in the south (Figure 2.1). The pattern is similar on both Bailey and Clark Peninsulas. It is likely that the poor development of vegetation on the southern aspects of the peninsulas is due to mesoclimatic features. The southern aspects receive less insolation than the northern, and consequently are colder for most of the year. Cold katabatic winds off the Vanderford Glacier are commonly from the south (Figure 3.2) and these may depress temperatures as well.

In the first published survey of vegetation from the Windmill Islands, Smith (1988a) identified 33 species of bryophytes and lichens from Bailey and Clark Peninsulas which occurred in 11 cryptogamic sociations. In a later, detailed survey of the entire Windmill Islands region, Melick *et al.* (1994) described the vegetation of the major sites of

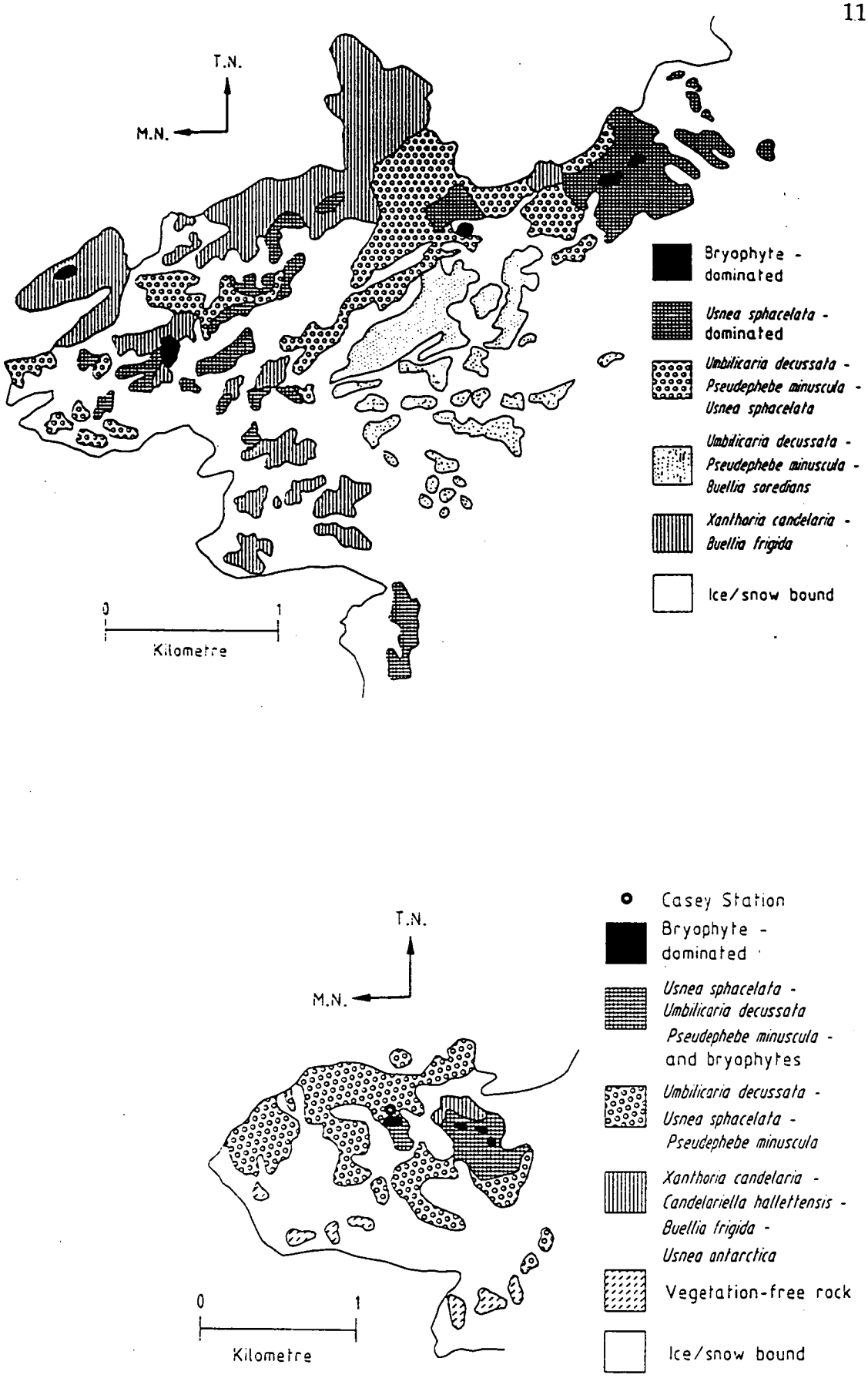

Figure 2.2 Distribution of major vegetation types on Clark (top) and Bailey (bottom) Peninsulas. From Melick *et al.* (1994).

Figure 2.3 Lichen dominated vegetation on Clark Peninsula showing extensive carpets of *Usnea sphacelata.*

lichen diversity as well as listing species present at all other sites. This study revealed that the development of vegetation was limited primarily by snow cover and site exposure. Lichens did not occur in sites which were snow bound for the majority of summer. Vegetation maps produced for the major peninsulas from a combination of aerial photography and ground survey identified five major vegetation types on Clark Peninsula comprising 27 lichen and 4 bryophyte species (Melick *et al.* 1994). The broadscale distribution of these vegetation types was shown to be related to the activity of penguins, aspect and proximity to the coast. Earlier studies correlated vegetation patterns in the area with substratum nutrient levels and water availability (Hancock & Seppelt 1988, Smith 1990). Smith (1990) also investigated the distribution and abundance of the principal bryophyte and lichen species in detailed transects along environmental gradients. On both Clark and Bailey Peninsulas the presence of abandoned penguin rookeries was found to have a marked effect on the distribution and abundance of species (Smith 1990, Melick *et al.* 1994).

2.2 The major lichen species

This thesis examines various aspects governing the nutrition, water relations, photosynthesis and distribution and abundance of the major elements of the terrestrial vegetation of the Windmill Islands region. The five major lichen species in this region, *Usnea sphacelata, Usnea antarctica, Umbilicaria decussata, Pseudephebe minuscula* and *Buellia frigida* are perhaps the most abundant macrolichens in Antarctica. Aspects of this study focus on the ecophysiological parameters of the three most obvious and dominant species, viz. *Usnea sphacelata, Umbilicaria decussata* and *Pseudephebe minuscula.*

Umbilicaria decussata (Figure 2.4) is a widely distributed foliose lichen which colonises bare, exposed rock faces as well as more sheltered drainage channels and even the sides of summer streams. In some localities in the Windmill Islands, *Umbilicaria decussata* is seen growing in run-off streams but it is absent from semi-permanently inundated sites. In some sheltered sites in the northern Windmill Islands *Umbilicaria decussata* grows to thallus sizes of up to 15 cm diameter. Of the three lichen species investigated, *Umbilicaria decussata* grew in the widest range of microhabitats. The genus *Umbilicaria* has been widely studied from all aspects (e.g. Larson 1982a,b, Sancho and Kappen 1989) and some

ecophysiological aspects of *Umbilicaria decussata* from the Windmill Islands region have been investigated recently (Melick and Seppelt 1994a).

Pseudephebe minuscula (Figure 2.4) is a fruticose lichen in which the thallus is often closely appressed to the substratum. It is almost always associated with *Umbilicaria decussata* but is seldom found in the same abundance except in the most sheltered of sites (Melick *et al.* 1994). In some areas in the northern Windmill Islands *Pseudephebe minuscula* grows in large monospecific stands. Although this species is one of the principal members of the most widespread plant assemblage in Antarctica (Smith 1988a), very little is known about its ecophysiology.

Usnea sphacelata (Figure 2.4) is a major component of much of the terrestrial vegetation of continental Antarctica (Kappen 1990). It is a fruticose lichen forming extensive carpets over metamorphic rocks and gravel beds in much of the northern Windmill Islands (Melick *et al.* 1994). The ecophysiology of *Usnea sphacelata* has been studied extensively (e.g. Kappen and Breuer 1991, Bölter *et al.* 1989) so it is a useful species for comparative purposes.

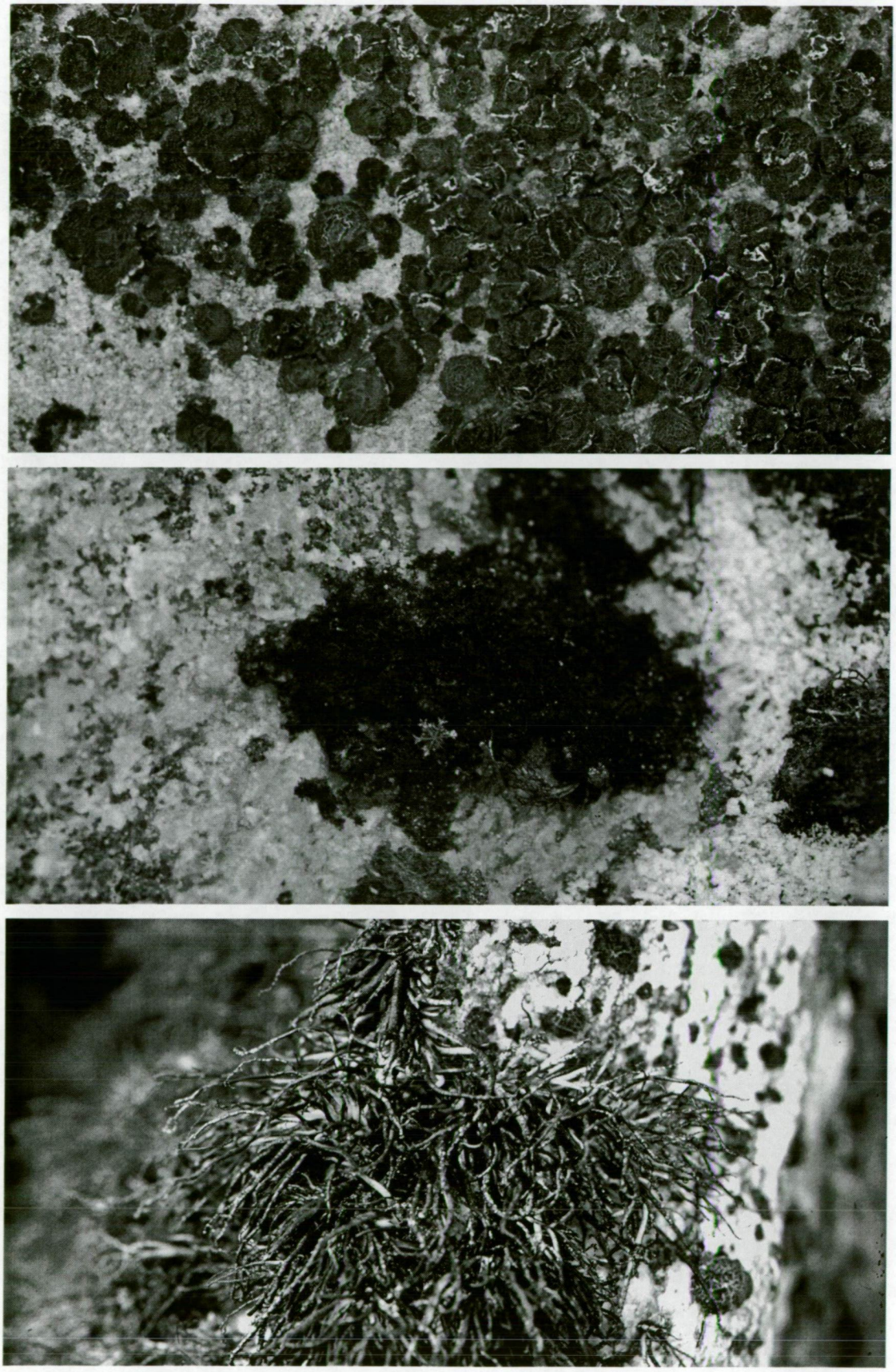

Figure 2.4 The three dominant macrolichen species in the Windmill Islands; *Umbilicaria decussata* (top), *Pseudephebe minuscula* (centre) and *Usnea sphacelata* (bottom).

Chapter 3

Microclimatic variation within the lichen habitat

3.1 Introduction

In any study of the interactions between the physiology and ecology of plants, the conclusions are dependant upon climatic conditions, since an organism's physiology is affected so markedly by its immediate environment. To this effect, many modern studies of plant ecophysiology contain some to many measurements of various climatic features of the site(s) where the study was done. Some of these measurements are simply made on an *ad hoc* basis whenever physiological readings are made, others present merely the local average conditions or the extremes. Better studies investigate microclimatic conditions for a certain period and relate these to physiological activity. Many of the more extensive data sets are based only upon local meteorological records. Despite the now widespread measurement of plant microclimates (see Jones 1992), there are relatively few comprehensive analyses of plant microclimate and its interaction with site and time of year, despite the enormous importance of this feature for a proper understanding of the distribution of plants.

In Antarctica, this is especially the case. Many researchers can only visit Antarctica for short periods over the summer and therefore present a snap-shot of the microclimate at a certain time of year. The winter conditions are harsh on automated equipment and regular checks are necessary to ensure continued operation, thereby limiting the number of year-round data sets to those where researchers or technicians are continuously present. Published investigations are limited to the climate and productivity of cryptoendolithic organisms in the dry valleys region (McKay and Friedmann 1985, Friedmann et al. 1987, 1993) and maritime mosses (Collins 1976).

It is also recognised that measurements of gross climatic data are, by themselves, insufficient for ecophysiological studies (Walton 1982). To this end biometeorological records have been divided into three major scales in this study: macroclimate, mesoclimate and microclimate. The macroclimate is that of a region and is based on the scale of kilometres

to hundreds of kilometres and is easily obtained from standard meteorological records which have been kept for decades, sometimes centuries. Mesoclimatic data cover a particular site and are generally considered to occur on a scale of somewhat less than a kilometre. These data need to be specially recorded unless the study site is very close to a meteorological station. The final, and most important, meteorological scale is that of the microclimate which occurs on the scale of centimetres to millimetres and generally is regarded as the exact conditions experienced by the organism. Instruments for measuring microclimate are specialised and need precise placement (Walton 1984). A finer scale, termed nanoclimate, is sometimes discussed and occurs on the scale of millimetres to micrometres, and considers, for instance, one side of a leaf as compared to the other, or the exact conditions which a particular cell experiences. Nanoclimatic data are extremely specialised and are not considered here.

Most of the data collected in this thesis come from one low, rounded knoll on Clark Peninsula, the northern-most peninsula in the Windmill Islands region. The vegetation on this knoll and its relationship to edaphic factors is described in detail in Ch. 7, and the seasonal changes in nutrient status of the dominant macrolichens of the site in Ch. 8. Water uptake of exposed lichens at the site is discussed in Ch. 6. This chapter describes the topography of the knoll and presents an account of the spatial and temporal variation in microclimatic conditions at this site, as well as considering local meso- and macroclimatic conditions.

3.2 Materials and methods

The knoll was mapped at a scale of 1:500 with a 0.5m contour interval from stereo pairs of aerial photographs taken in mid-summer 1993-94. The snow cover at this time of year is minimal and most of the macrovegetation was exposed.

In April 1992 an Aanderaa 3010 microclimate station was installed near the summit of the knoll (Figure 3.1). This station included sensors for measuring ambient temperature, net atmospheric radiation and solar radiation as well as six thermistor probes for the measurement of temperature in the lichen microhabitat. The whole assembly was powered by a long life lithium battery and data were stored on a

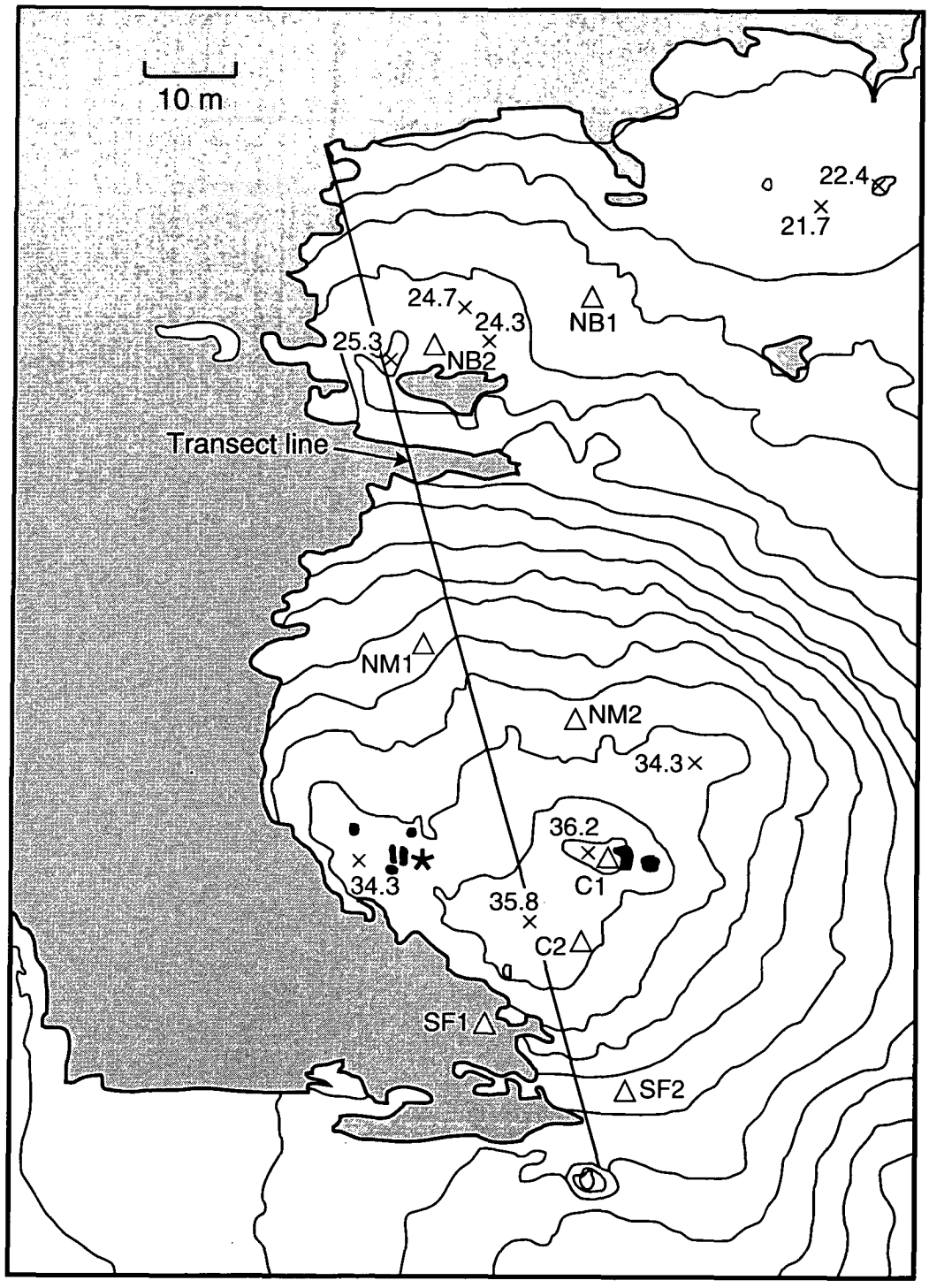

Figure 3.1 Topographic map of the study knoll on Clark Peninsula. Contour interval 1m.
✱ = site of the microclimate station
△ = sites of measurement, with abbreviations as defined in the text.
X = spot heights in metres.
▒ = late-lying snow.

specialised data storage unit. This unit can store up to two years' worth of data, but the units were changed monthly until the end of February 1993 when I returned to Australia. The storage unit was then left in place until November 1993 when I returned to the study site. The storage units were interrogated by a personal computer using specialised software in the laboratory. The six thermistor probes were located in various positions across the knoll. Two probes were placed in the middle of the northern slope (sites NM1 and NM2), two in the crest region (C1 and C2) and two on the southern slope just below the crest region (SF1 and SF2). Two additional thermistor probes were placed at the base of the northern slope connected to a Grant Squirrel SQ2 data logger (NB1 and NB2). This data logger was powered by long life 9V batteries, changed monthly, and each month downloaded in the field with a laptop personal computer using specialised software. All of these probes were placed amongst lichen thalli and were, at all times, in direct contact with thalli of *Usnea sphacelata*. The measuring positions are shown on Figure 3.1.

Additional measurements were made of photosynthetic photon flux density (PPFD) both above and under the snow from late winter to early summer. These measurements were made with two LiCor LI-190SB quantum sensors logged by a LiCor LI-1000 data logger using a 60s integration period and recording maximum, mean and minimum PPFD every 30 min.

Macroclimate data were obtained from Bureau of Meteorology measurements made at the Antarctic Meteorology Centre on Bailey Peninsula, approximately 2.5km to the south of the study site. These records were made by professional observers taking readings every three hours. Daily cloud cover observations were made at 9:00 am local time and recorded in octas (one-eighth sectors of the sky, i.e. eight octas corresponds to total cover).

3.3 Results

The crest of the knoll is 36.2 m above sea level. Figure 3.1 is a contour map of the site showing the location of various features including the measurement sites. The knoll consists mainly of metamorphic shists and gneisses with occasional granitic erratics occurring near the summit. The substratum structure and chemistry is described in detail

in Ch. 7. The map (Figure 3.1) shows the presence of a semi-permanent snow/ice bank to the west of the knoll and a permanently ice-filled valley to the north. The snow bank continues around to the southern edge of the knoll's crest for most of the year, disappearing only in mid-late summer.

MACROCLIMATE

The climate of the Casey region is frigid-Antarctic (*sensu* Longton 1988). The mean monthly temperatures are low and gale-force winds occur virtually every month. The monthly macroclimatic conditions from April 1992 to February 1993 are shown in Table 3.1. Snow fell on 80% of the days in the measuring period, the mean cloud cover was 5.6 octas and the mean daily number of hours of sunshine was 2.4. During August the wind-run anemometer froze and had to be replaced, hence there is no mean wind speed for that month. Figure 3.2 is a wind-rose for the five year period up to 1992 showing the frequency and direction of moderate and gale force winds. It is obvious that moderate winds come predominantly from the south and north-east while almost all of the gale force winds come from the east.

TABLE 3.1 Monthly macroclimatic details for the period from April 1992 until February 1993.

	Temperature (°C)			Wind speed (knots)		Days of snow
	Mean	Max.	Min.	Mean	Max.	
April	-11.3	-0.4	-23.5	10.6	73	20
May	-16.1	-0.7	-33.8	8.3	50	13
June	-11.8	4.2	-25.5	14.9	89	16
July	-16.3	-2.5	-32.4	8.7	116	16
Aug.	-12.4	0.2	-28.9		110	16
Sept.	-16.3	-2.3	-29.9	18.3	96	13
Oct.	-12.8	-1.7	-31.2	13.2	115	18
Nov.	-1.4	5.4	-8.5	8.0	53	14
Dec.						
Jan.		6.9	-8.5	14.6	79	10
Feb.		4.7	-5.9	14.3	82	17

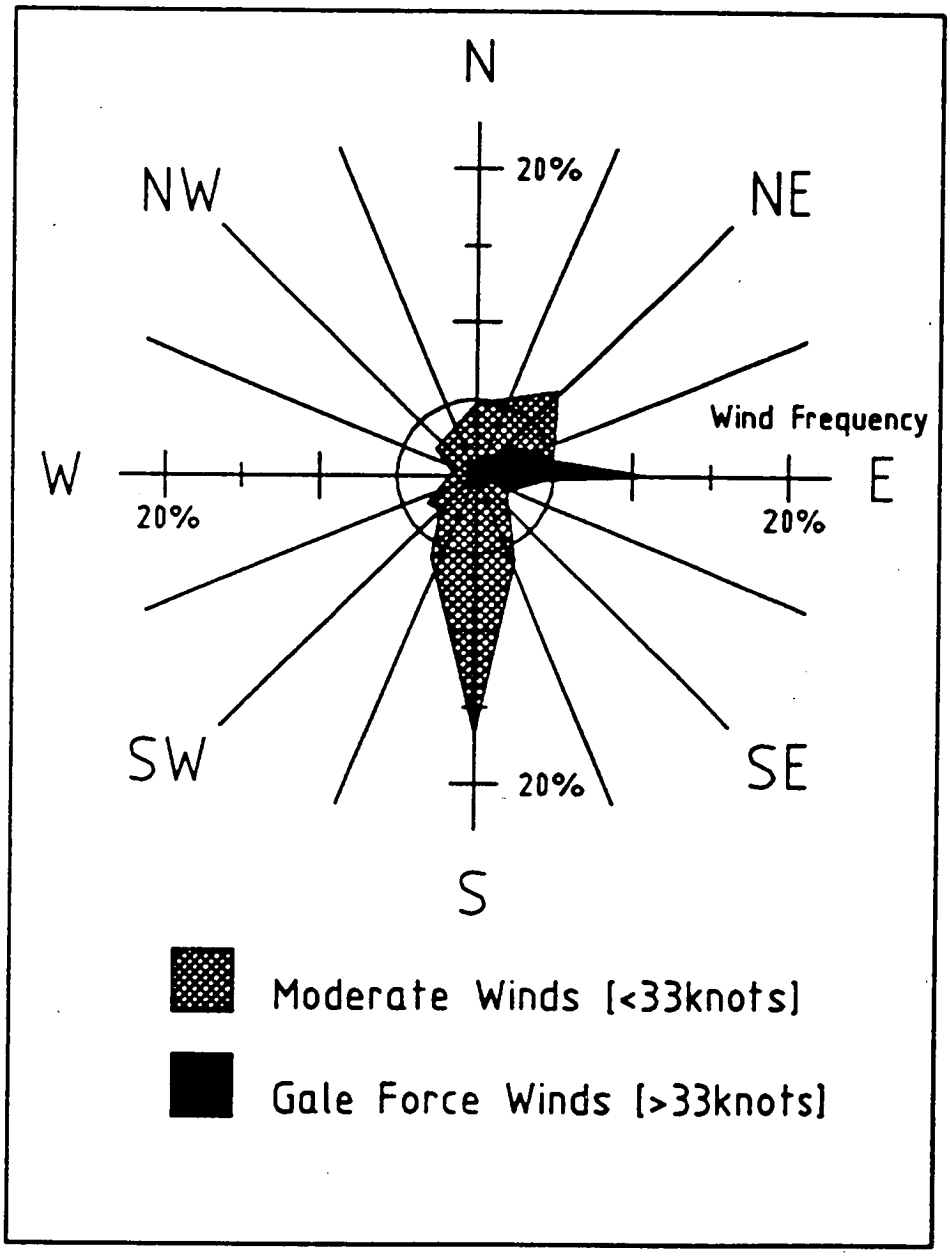

Figure 3.2 A wind-rose showing the frequency of direction for various wind strengths for the five years of meteorological records up to 1992. The circle shows the % frequency of calms. From Melick *et al.* (1994).

MESOCLIMATE

Data are only available for the period from April 1992 to February 1993. When the data storage unit was interrogated in November 1993, no useful data were obtained. This failure of the data storage unit was unfortunate since it prevented the analysis of conditions from two consecutive winters.

From April 1992 to February 1993, the exposed flat crest region of the knoll had a net positive radiation balance of some 633.8 $MJ.m^{-2}$, which consisted of 317.4 $MJ.m^{-2}$ of direct solar radiation and 316.4 $MJ.m^{-2}$ of scattered or atmospheric radiation. Although these values are almost exactly the same, the distribution of this radiant energy over the summer was not even, with the highest input of solar radiation occurring during November and the highest level of atmospheric radiation occurring during January. The average daily solar and atmospheric radiation balance for each month and their relation to average number of sunlight hours per day and average cloud cover are presented in Figure 3.3. Direct insolation was greatest in November, which was the summer month with the lowest mean cloud cover. The radiant flux density ranged from -10 $mW.cm^{-2}$ to approximately 300 $mW.cm^{-2}$ (Fig 3.4).

The mesoclimatic ambient temperature for the knoll is presented in Figures 3.5 and 3.6. The ambient temperature range during the measuring period was from -33.5°C to 8.9°C with a mean temperature -9.0°C. Diurnal variations in ambient temperature were generally slight with a mean diurnal temperature difference of 5.2 K and a range from 0.26 K on 6/7/92 (-11.25°C to -10.99°C) and 11/9/92 (-7.62°C to -7.36°C) to 20.4K on 12/10/92 (-31.6°C to -11.2°C). Even in mid-summer, the ambient temperature was regularly below zero, with only 27 days in the entire year having temperatures above zero all day, most of these occurring in January. In mid-June an unusual blizzard caused the ambient temperature to increase to more than 0°C and remain there for 60 hours, after which the temperature rapidly dropped to well below freezing point. This midwinter anomaly is evident on Figures 3.5 and 3.6, and is discussed in detail in Ch. 8.

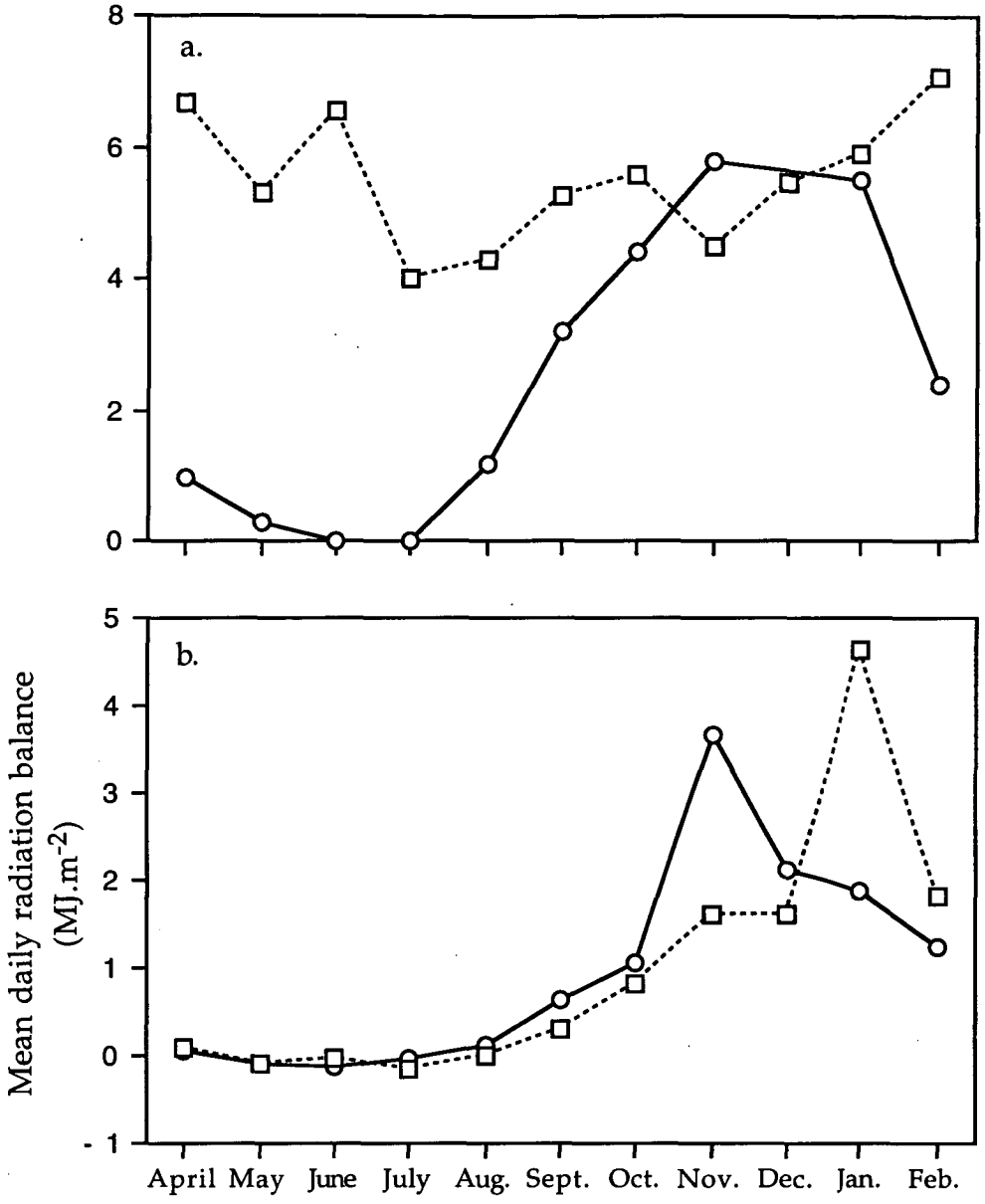

Figure 3.3. (a) Mean daily cloud cover in octas (squares) and mean daily hours of sunshine(circles). (b) Mean daily solar (circles) and atmospheric (squares) radiation flux.

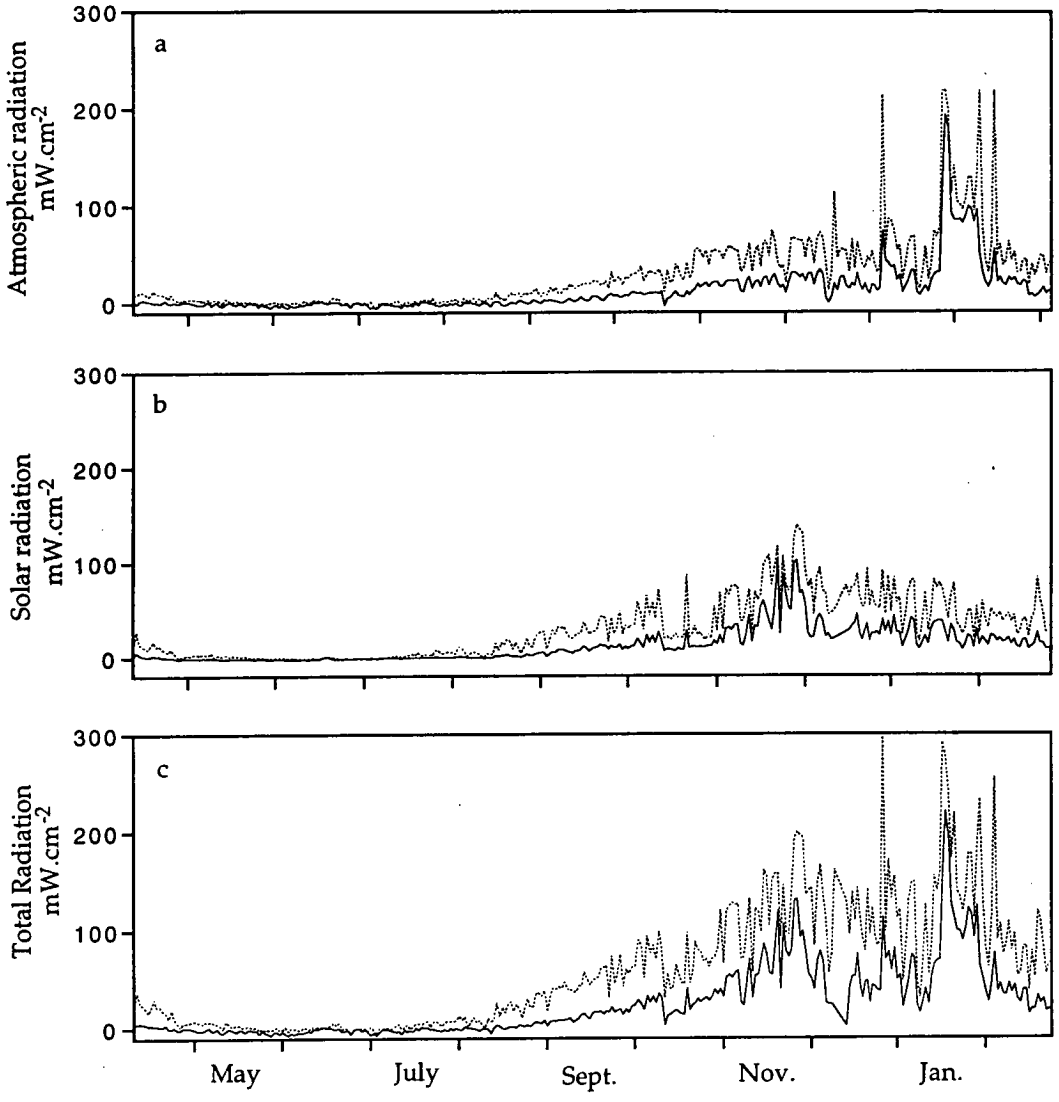

Figure 3.4 Daily mean (solid line) and maximum (dotted line) radiant flux densities for (a) atmospheric radiation (b) solar radiation and (c) total radiation.

MICROCLIMATE

Thallus temperatures ranged enormously over the period of the year and from site to site. During the months of April to September, with one very noteworthy exception, thallus temperatures never exceeded 0°C. The exception was during and immediately after the warm temperature anomaly in mid-June. The relatively high ambient temperature at this time caused thallus temperatures to increase rapidly at all sites. The reasons for this anomaly and its biological consequences are discussed in detail in Ch. 9.

The daily mean, maximum and minimum thallus temperatures for all eight sites are given in Figures 3.5 and 3.6. The highest thallus temperatures were experienced by lichens on the north-facing slope (NM) and the lowest by those in the exposed crest region (C2). Mean, maximum and minimum thallus temperatures for the measuring period are presented in Table 3.2. The patterns in thallus temperatures are markedly different between the summer and winter months at all sites (Figure 3.5 and 3.6). There is little diurnal variation in temperature between the months of April and September at all sites, and until late December at the SF1 site. From October until February, the diurnal differences in thallus temperature (ΔT) are generally large, being greater in the north facing and crest sites than in those facing south. The maximum ΔT occurred at the C2 site on 31 October and was 41.3K. The maximum ΔT values for both the C1 (35.4K) and NM2 (39.5K) sites also occurred on this day. The ΔT values for the other sites were smaller, being 31.7 K for NM1, 19.9 K for SF1 and 20.2 K for SF2. These values occurred on 3 January, 12 January and 10 January respectively.

The number of freeze-thaw cycles varied considerably between sites. Table 3.3 shows the total number of cycles for the measuring period where the daily temperature range is greater than +0.5°C to -0.5°C and +0.5°C to -2.0°C. The temporal distribution of these freeze-thaw cycles can be seen in Figures 3.5 and 3.6. The freeze-thaw cycles extend through the summer period but begin at different times, resulting in the differences seen in Table 3.3. During winter, with the exception of the unusual event in mid-June, thallus temperatures never approached 0°C.

TABLE 3.2 Mean, maximum and minimum thallus and ambient temperatures for the period of April 1992 until February 1993 for the study knoll on Clark Peninsula. The site names refer to those indicated on Figure 3.1. Data loss at sites NB1 and NB2 prevented the calculation of statistics at these sites.

Site	Mean T (°C)	Max. T (°C)	Min. T (°C)
Ambient	-9.0	8.9	-33.5
NM1	-7.8	32.3	-28.6
NM2	-9.4	32.8	-39.4
C1	-9.7	29.2	-40.3
C2	-9.9	30.4	-44.1
SF1	-9.5	20.0	-24.1
SF2	-7.5	22.7	-29.5

The results for the NB1 and NB2 sites are marred by lack of data due to equipment failure. Both the probes themselves, for the NB2 site, and the data logger malfunctioned several times giving rise to gaps in the data. There was also a problem with measurements of high and low thallus temperatures, with the probes returning a constant value when thallus temperatures were either greater than 26°C or less than -26°C. For that reason, ΔT, mean, maximum and minimum temperatures and the number of freeze-thaw cycles were not calculated for these sites. The data are plotted on Figure 3.5 for comparative purposes and show similar patterns to those for the NM sites.

TABLE 3.3 Number of freeze-thaw cycles occurring between April 1992 and February 1993 at six sites on the study knoll and in the air. The data sets for NB1 and NB2 were insufficient for calculations.

Site	-0.5 to 0.5°C	-2.0 to 0.5°C
NM1	53	33
NM2	93	71
C1	100	80
C2	114	97
SF1	40	21
SF2	54	34
Ambient	51	22

PPFD under the snow was generally lower than that above the snow. For comparative purposes, PPFD was divided into five categories: <10 $\mu mol.m^{-2}.s^{-1}$, 10-50 $\mu mol.m^{-2}.s^{-1}$, 50-100 $\mu mol.m^{-2}.s^{-1}$, 100-500 $\mu mol.m^{-2}.s^{-1}$ and >500 $\mu mol.m^{-2}.s^{-1}$. Figure 3.7 shows the number of hours each day that a lichen in either exposed or snow-covered sites on the flat crest region would have been exposed to each category of PPFD. The cover of snow started at 30 cm and gradually decreased, increasing again with heavy snow-falls in late September/early October and early November. During the middle of October the snow cover in the crest region was negligible. The cover of snow kept PPFD generally below 500 $\mu mol.m^{-2}.s^{-1}$ and increased the amount of time when PPFD was low (<50 $\mu mol.m^{-2}.s^{-1}$) while having little effect on the duration of exposure to intermediate PPFD.

Data logger technical problems resulted in loss of some data during the measuring period, and complete break-down after early November. The logger was repaired and used for short periods on Bailey Peninsula after this (see Ch. 5).

3.4 Discussion

The crest of the knoll is the highest point heading in an easterly direction until the Løken moraine is reached and is therefore exposed to the predominantly easterly winds (Figure 3.2). Therefore the crest region and the eastern face of the knoll are often subject to gale-force, abrading winds. Most snow is scoured from the eastern face and crest regions while the topography results in wind-driven snow accumulating on the western side of the knoll and in the lee of some small ridges and large boulders. This pattern of snow accumulation results in a variety of microclimatic conditions across the knoll which vary in their response to changes in the macro- and mesoclimate. Snow cover was not recorded quantitatively because of large day to day variability, however, in retrospect it would have added to the importance of the data set had snow depth been measured regularly.

Aspect also has a direct role in the form of interception of direct solar radiation. The total radiation incident on the site consists of almost equal quantities of direct solar radiation and atmospheric or scattered radiation. That part of the net radiation flux which is scattered from the sky is little affected by aspect since illumination from an even

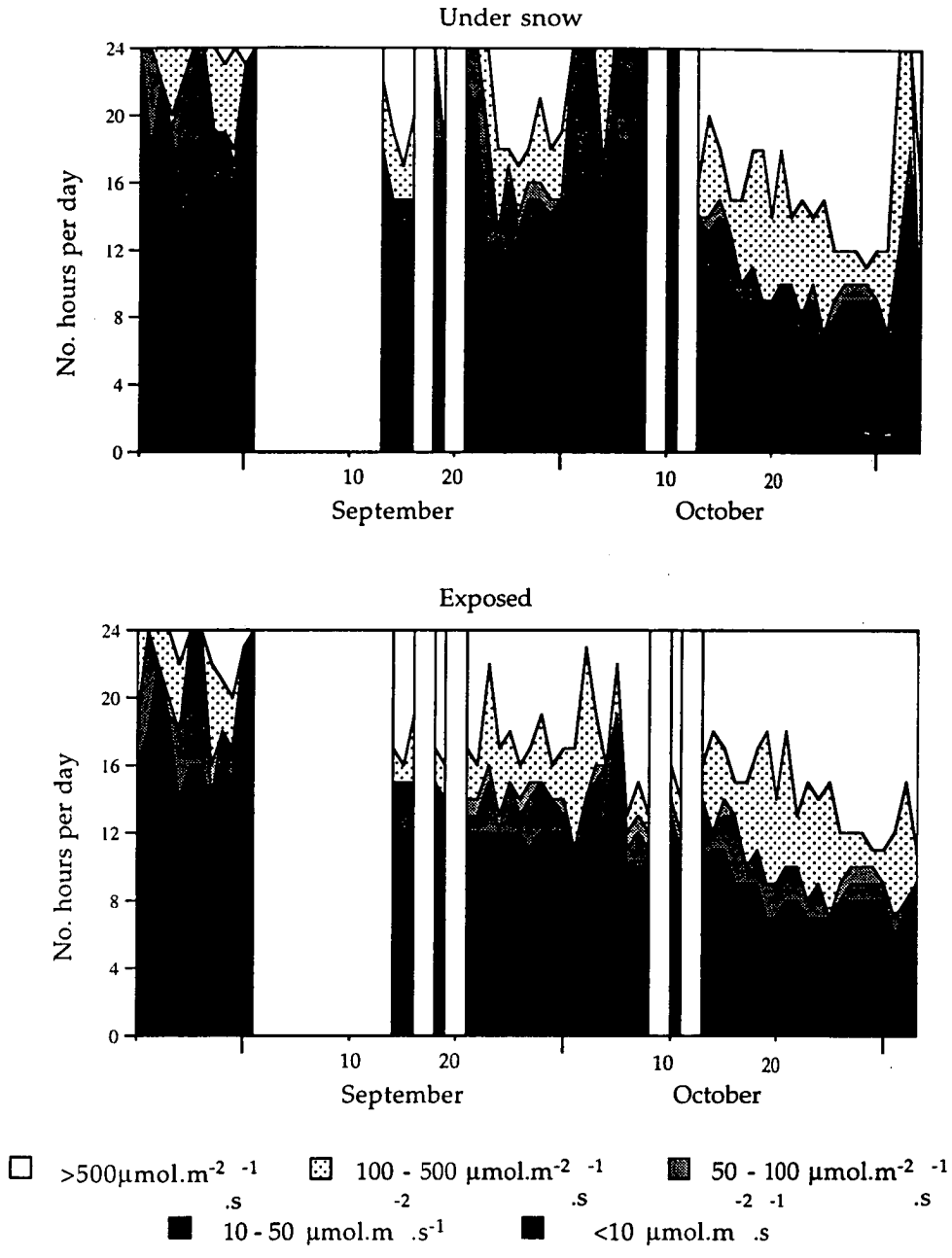

Figure 3.7 The daily number of hours for which lichens under snow (top) or exposed (bottom) receive different PAR levels.

cloud cover is generally uniform at the surface. Radiation which is reflected from the surrounding snow and ice, however, would be unevenly distributed and therefore the amount incident at any one microhabitat would depend on the amount of snow surrounding the site as well as aspect. In general, those sites facing eastward would receive a great deal of radiation reflected from the snow and ice of the greater Antarctic plateau, while those on the western and northern slopes would receive radiation reflected from the snow bank and ice-filled valley. The solar radiation flux of each site is strongly affected by aspect, especially given the high latitude of the region, with the south-facing slopes receiving much less direct insolation than the north-facing slopes. The radiation balance of the site is, therefore, an approximation since data were collected from one site in the flat crest region of the knoll. While these data are excellent for the C1 and C2 sites, the other sites will probably receive slightly different amounts of both net atmospheric radiation and solar radiation due to aspect. However, since one pyranometer and one solarimeter were all that was available, and since the sensors were positioned centrally, the data provide quite a resonable estimate of the mesoclimatic radiation balance.

The total net radiation flux at the site was lower than that reported for the maritime regions of Antarctica (Walton 1984). This can be attributed to the substantially higher input of solar radiation at all times of the year (Longton 1988). I am not aware of any other records for annual radiation balance of a continental Antarctic site but short-term summer records of solar radiation from Ross Island (Longton 1974) show very similar values to those reported here. Bintanja (1995) provided detailed radiation data for the surface of a glacier in the maritime Antarctic for a short period in summer. Those results show the effect of the high albedo of the glacier surface, but are otherwise similar to those presented here, with an important contribution of atmospheric radiation due to the frequent overcast conditions.

Thallus temperatures showed distinct patterns, which were typical of their season. In winter the lichen thallus temperature exhibited little difference between day and night and remained well below freezing, while in summer thallus temperatures fluctuated widely from day to night, often exceeding 20°C in the day and falling below 0°C at night. The magnitude of these diurnal patterns differed between sites, mostly

due to the combination of exposure and interception of direct solar radiation. The onset of summer conditions also varied with site and can be directly related to the patterns of late-lying snow (see below).

From the investigation of thallus temperatures it is evident that the transition from winter to summer conditions is abrupt. Unfortunately, the loss of the data from March 1993 onwards prevents the comparison of the transition from summer to winter conditions, although it is clear that by early April 1992 thallus temperatures showed little diurnal variation and stayed well below freezing. Therefore we can reasonably assume that the transition from summer to winter is equally as rapid as that from winter to summer, with very little evidence of a spring or autumn. Microclimatic temperature data from the maritime Antarctic (Davey *et al.* 1992) show a definite autumnal period from mid-February to mid-May, at which time the temperature was stable around 0°C, with little diurnal variation. While it is possible that this may have occurred on Clark Peninsula during March, the only month for which no microclimate temperature data are available, there is no evidence of extended stable conditions. Indeed, it is possible that the conditions described in autumn 1987 at Signy Island were atypical, since there is no evidence of this having occurred at King George Island (Schroeter *et al.* 1995).

Variation in thallus temperatures between sites can be explained by an interaction of their interception of solar radiation and snow cover. Of the eight sites, that with the least accumulation of snow was the C2 site which was the most exposed and therefore subject to the greatest amount of wind scour. This site had the greatest diurnal variation in thallus temperature as well as experiencing the lowest actual thallus temperature during the year. Conversely, SF1 had the greatest accumulation of snow and consequently showed negligible diurnal variation in thallus temperature for most of the year. The nearby SF2 site which had less snow accumulation during winter exerienced much lower minimum temperatures and a great deal more diurnal variation, particularly in early summer. After the snow bank at SF1 had melted in late December, the two south facing sites showed few differences in thallus temperature. The presence of the snow bank at SF1 well into summer resulted in a depressed average thallus temperature at this site, despite the protection from the exteme low temperatures.

Snow accumulation on the north facing slope was greater at NM1 than at NM2 and consequently the diurnal variation in thallus temperature was greater at NM2 for much of the year. While the two sites experienced near to identical conditions through the summer, the accumulation of snow protected lichens at NM1 from the lowest temperatures. The onset of high thallus temperatures was also delayed at NM1 by snow cover and therefore the number of freeze-thaw cycles to which lichens at NM1 were exposed to was considerably lower than for those at NM2. The two south-facing sites were exposed to far fewer freeze-thaw cycles than those on the crest.

The number of freeze-thaw cycles recorded at the study knoll was substantially greater than has been reported for lichens from the maritime Antarctic regions (Davey *et al.* 1992; Schroeter *et al.* 1995). In both these Maritime cases, lichen thallus temperatures in summer were generally above 0°C, so the number of freeze-thaw cycles in this part of the year would be much lower. Freeze thaw cycles did occur during winter on King George Island (Schroeter *et al.* 1995) but not on Signy Island (Davey *et al.* 1992). When a freeze-thaw cycle was defined as a change in temperature from -2.0 to +0.5°C, instead of the narrower -0.5 to +0.5°C definition, the annual number of freeze-thaw events in *Usnea* vegetation on Signy Island fell to only 14, which is a fraction of the minimum number recorded for the study site at Casey. Other studies of lichen activity in relation to microclimate from the Windmill Islands (Bölter *et al.* 1989; Kappen & Breuer 1991; Kappen *et al.* 1991) showed that during summer lichen thallus temperatures regularly passed through 0°C. In contrast to this, the number of freeze-thaw cycles in moss communities on Signy Is. was much greater than those reported for lichens in the same region (Longton 1988). Indeed, the maximum frequency of freeze-thaw cycles in 1965-66 in dry moss turves (110 cycles of -0.5 to 0.5°C in 12 months, Longton 1988) was almost as great as at the crest sites here. The reasons for this may be partially attributed to microsite, but must also be due to particularly severe macroclimatic conditions in that year, since the number of freeze-thaw cycles at the same site did not approach such high levels in any other year measured.

An accumulation of snow also reduces the penetration of PPFD. Given that, in most cases, snow banks disappear during early summer, the microclimate under a moderate depth of snow will exhibit slight

diurnal changes in thallus temperature, will be warmer than exposed sites at times of extremely low ambient temperature and have generally lower levels of PPFD in early summer. The relative advantages and disadvantages of these conditions will be discussed in Ch. 9.

Chapter 4

Photosynthesis of Antarctic Lichens and its Measurement

4.1 Lichen Photosynthesis and its Interaction with Thallus Water Content.

The study of photosynthesis of lichens commenced early this century (see Stocker 1927), and since then has been largely an investigation of the relationship between carbon exchange of the symbiosis and variables such as thallus water content (WC), thallus temperature and photosynthetic photon flux density (PPFD). Since the lichen symbiosis contains both photobiont and mycobiont, there are several sources and fates of CO_2 in the symbiosis. Many of the investigations of lichen carbon relations have neglected this fact, considering the symbiosis as a plant to the point of treating the observed CO_2 assimilation as the net photosynthesis of the lichen. In reality, the observed patterns of CO_2 exchange will be the consequence of CO_2 assimilation by photobiont photosynthesis minus the CO_2 output of mycobiont respiration, photobiont mitochondrial respiration and photobiont photorespiration. Research on the photosynthetic relations of vascular plants usually deals with activity in the leaves or stems, largely ignoring root respiration, and definitely ignoring loss of carbon to mycorrhizal fungi. Honegger (1991) has argued that a lichen is essentially a mycorrhizal plant in a sealed environment in which the surrounding CO_2 concentration remains fairly constant despite the photosynthetic activity of the photobionts. This argument, although not supported by experimental data, presents a viewpoint which casts doubt on the validity of measurements of the CO_2 exchange of a water saturated lichen.

The study of CO_2 assimilation of the symbiosis is further complicated by interactions with other variables. For example, the interaction of carbon exchange with WC has been studied extensively in lichens from a range of habitats (Lange 1969, Kershaw 1971, Lange and Matthes 1981, Nash *et al.* 1990, Schroeter *et al.* 1991*a*). Investigators of lichen CO_2 exchange as a function of WC have been fascinated by the apparent inhibition of net photosynthesis by high WC. Lange *et al.* (1993*a*) have recently classified lichen photosynthetic response to WC into four categories based on the presence and extent of assimilation

depression at high WC. Figure 4.1 shows the relationship between net assimilation and WC in the four types identified so far. Response D, in which a severe depression of carbon assimilation occurs at high WC but net CO_2 loss does not occur, is the most common relationship observed and the only response published so far for continental Antarctic lichens. In all species investigated, there is a minimum WC for photosynthetic activity, the water compensation point, below which CO_2 exchange is zero or negative (Lange *et al.* 1990).

Despite extensive study, there has been confusion as to the cause of inhibition of net photosynthesis by high WC. When lichens are water-saturated the resistance to gas exchange becomes enormous. The rise in resistance to gaseous diffusion between the surrounding atmosphere and the photobionts caused by increasing WC has been demonstrated conclusively (Cowan *et al.* 1992), yet there remains debate on whether this increase in resistance to CO_2 diffusion causes the observed drop in CO_2 assimilation. If the photobiont photosynthetic rate was maintained at a constant level from the optimum WC to the saturation WC, the observed depression in carbon assimilation may be due to the predominance of fungal respiration at supraoptimal WC. However, if this were true the internal CO_2 concentration would increase and the actual rate of photobiont photosynthesis would rise due to this increase, as well as the concomitant drop of internal oxygen tension, which has been shown to occur (Millbank 1977, Hovenden pers. obs.). Gas exchange analysis would fail to discern this change in actual photobiont photosynthesis, although this would only occur in species in which respiration rises indefinitely with increasing WC (Harrisson *et al.* 1986). It has also been argued (Honegger 1991) that CO_2 produced by the mycobiont in these conditions might be a major source of carbon for fixation by the photobionts and conventional gas exchange analysis is unable to account for this, thereby underestimating the actual photosynthetic rate.

4.2 Rehydration of dry thalli

Since photosynthetic activity of lichens is dependent upon the level of thallus hydration, much interest has been generated by the observation that lichens with green algal photobionts are able to re-activate photosynthesis by absorbing water vapour from a humid

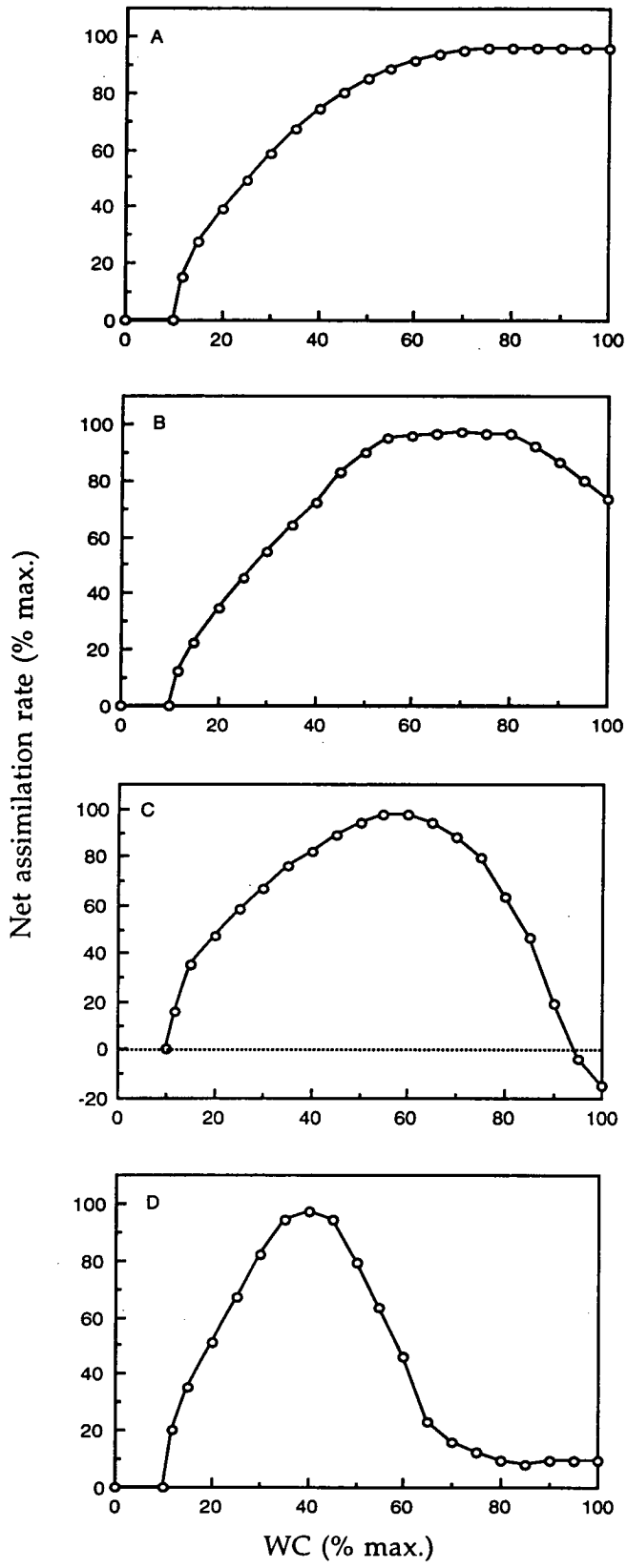

Figure 4.1 Lichen assimilation rates as a function of thallus water content (WC) for four imaginary thalli illustrating the response categories (A)-(D) defined by Lange *et al.* (1993a).

atmosphere (e.g. Kershaw 1985, Lange and Kilian 1985, Lange *et al.* 1986, 1989) while those with cyanobacterial photobionts are unable to do so (Lange *et al.* 1993*b*). The investigations which have yielded the greatest amount of information on the actual photosynthetic state of the photobionts have involved modulated fluorescence analysis to study quenching coefficients and fluorescence induction curves of lichens when desiccated, during exposure to humid air and after addition of liquid water (Lange *et al.* 1989) (see section 4.3 for a discussion of chlorophyll fluorescence analysis). The results show that in *Ramalina maciformis* (Del.) Bory (green algal photobiont) there is no difference in the fluorescence characteristics when rehydrating from a humid atmosphere compared with when dehydrating after wetting with liquid water. Fluorescence induction of *Peltigera rufescens* (Weiss) Humb. (cyanobacterial photobiont) only occurred after the addition of liquid water, even after prolonged exposure to high humidity. A mechanistic interpretation for these species, which involves differential reversibility of a functional interruption of energy transfer between LHCII and the PSII reaction centre, has been proposed by Bilger *et al.* (1989). These studies have sometimes been regarded as indicative of all lichens, including those which occur in polar regions. Laboratory experiments with *Usnea sphacelata* from continental Antarctica (Kappen 1983) showed that this species re-initiated photosynthesis after exposure to >96% RH for 60 h. It has been assumed that continental Antarctic lichens in the field can absorb sufficient water from a humid atmosphere to re-initiate photosynthesis, since there are no known continental Antarctic lichens with cyanobacterial photobionts. This assumption has been crucial to models of photosynthetic activity of Antarctic lichens (Bölter *et al.* 1989, Kappen *et al.* 1991) and the corresponding growth and age estimations (Kappen 1990). Field investigations of 12 species of lichens in continental Antarctica (Gannutz 1967) have shown that only one could derive sufficient moisture from humid air to fix carbon. Despite its importance, the question of reactivation of lichen photosynthesis in Antarctica due to water vapour uptake is as yet not unequivocally answered.

4.3 Chlorophyll fluorescence analysis.

When a photon is absorbed by a pigment molecule associated with a photosystem, the excitation energy is transferred to the reaction centre of that photosystem. This excitation energy is released when the

excited electrons return to ground state and may be used by the photosystem reaction centre to generate charge separation, and therefore to drive electron transfer and the synthesis of ATP and NADPH. This energy may also be lost as heat or re-emitted through a process known as fluorescence. It appears that most of the fluorescence of a functioning, intact leaf originates in the chlorophyll *a* antenna of PSII. The analysis of this chlorophyll *a* fluorescence provides a direct indication of the functioning of the intact photosynthetic apparatus. The monitoring of the induction of fluorescence in a dark-adapted leaf generates a characteristic fluorescence induction curve, or Kautsky curve (Figure 4.2). This curve has two phases which correspond to two separate sets of photosynthetic processes, one in the millisecond scale and the other in the second to minute scale, usually referred to as fast kinetics and slow kinetics respectively. The analysis of this curve gives the fluorescence parameters so often used. These parameters are indicated on Figure 4.3. F_o is the initial or minimal fluorescence of a dark adapted leaf produced by the measuring light. A leaf in this state has nearly all of its PSII reaction centres open. When the leaf is exposed to strong light the fluorescence level rises to a maximum (F_m) and then begins to decay (Figure 4.2b). The difference between F_m and F_o is termed the variable fluorescence (F_v). The use of a modulated fluorometer provides further information on the state of the photosynthetic apparatus, since it uses a separate modulated measuring beam of very low intensity and can therefore be used in illuminated conditions. As would be expected, the parameters measured in an illuminated state differ markedly from those measured in dark adapted leaves. The parameters corresponding to maximal and minimal fluorescence levels in a light adapted sample are designated F'_m and F'_o, respectively. The instantaneous fluorescence at time t is F_t. The difference between F'_m and F_t is designated ΔF. Figure 4.3 illustrates these parameters. One of the most interesting applications of fluorescence quenching analysis is the measurement of the Genty parameter, $\Delta F/F'_m$, which is an estimate of the photochemical quantum yield of PSII (ϕ_{PSII}) (Genty *et al.* 1989, Edwards & Baker 1993).

The advent of the fluorometer has been a boon to ecophysiological studies. Measurements are rapid and non-destructive, and have proved a useful tool for the investigation of direct effects on photochemical activity, as well as those of various physiological

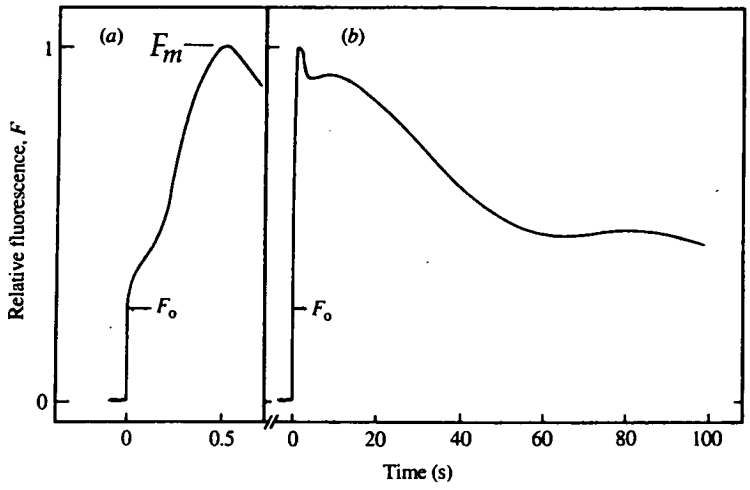

Figure 4.2 Characteristic fluorescence induction kinetics (Kautsky curve) on illuminating a dark-adapted leaf, showing the very rapid rise to F_0 followed by fairly fast rise to a maximum (F_m), followed by slower decay to a steady state as photosynthesis starts up: (*a*) fast kinetics, (*b*) slow kinetics. (Adapted from Jones 1992).

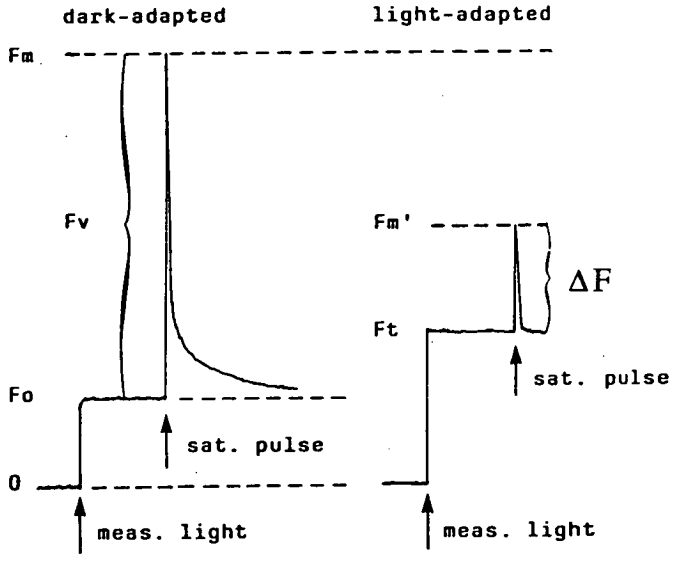

Figure 4.3 Fluorescence parameters in dark-adapted and light-adapted leaves, as explained in the text. (Adapted from Walz 1993).

constraints, such as droughting and chilling injury. Early investigations of the Kautsky curve concentrated on the use of fluorescence quenching as a diagnostic probe of phenomena such as photoinhibition (Critchley and Smillie 1981, Krause and Weis 1984). The advent of "stress meters" allowed the rapid determination of fluorescence quenching parameters, especially the ratio of variable to maximal fluorescence, the F_v/F_m ratio, which has been shown to be an indicator of photosynthetic efficiency (Demmig and Björkman 1987). The modulated fluorescence technique, which allows fluorescence monitoring in the presence of continuous light and therefore the investigation of plants in a naturally illuminated state, has proved even more useful (Schreiber and Bilger 1987). Modulated fluorometers allow the determination of the photochemical, q_P, and non-photochemical, q_N, coefficients of fluorescence quenching, as well as photochemical quantum yield, ϕ_{PSII}, and the regular Kautsky curve. The investigation of photosynthetic parameters by various fluorescence techniques has been discussed by Bolhàr-Nordenkampf *et al.* (1989) and Jones (1992).

All fluorescence results presented in this thesis were obtained using the PAM-2000 portable modulated fluorescence system (Heinz Walz GmbH, Effeltrich, Germany). The PAM-2000 is a reasonably recent invention, combining the advantages of the older laboratory-based, modulated fluorometers with portability and ease of use. The unit is small and light and contains all the different light sources and controls as well as a power source. The PAM-2000 is operated through a palm-top personal computer which controls the fluorometer's functions, as well as logging and analysing the output. The computer calculates all fluorescence parameters and displays the results on-screen. The system is usually operated with a fibre-optic cable which allows the measurement of leaves or thalli at virtually any angle or position. The head of the fibre-optic cable can be mounted in either a distance-clip or leaf-clip, both of which keep the fibre-optic head at a set angle of 60° to the sample, and at a constant, yet variable, distance from the sample. The leaf clip also contains a micro-quantum sensor for the measurement of PPFD and a NiCr-Ni thermocouple for the measurement of leaf temperature. The nature of the lichen thallus prevented the use of the leaf clip except when studying *Umbilicaria decussata* in the laboratory. In all other cases the distance clip was used.

4.5 Lichen Photosynthetic Activity Measured using Modulated Fluorescence

Investigation of fluorescence quenching characteristics provides information on the exact photosynthetic state of the photobiont. The earliest measurements of lichen photobiont fluorescence involved lichens at a range of hydration levels. Thalli were frozen, ground into a powder and the fluorescence spectra were observed at 77K (Jensen and Feige 1987). Other early studies also investigated fluorescence spectra at 77K (e.g. Velly and Leclerc 1987). These studies were able to demonstrate differences in the fluorescence spectra of lichens at different hydration states and between lichens from different habitats. The rigorous conditions necessary for these investigations limited the comparisons between fluorescence results and conventional photosynthetic investigations, but the step provided insight into the function of lichen photobionts.

The investigation of the Kautsky curve at ambient temperature, particularly the F_v/F_m ratio, began to give insight into the state of photobionts when the lichen was in a reasonably "normal" state. Unfortunately some of the early investigations of fluorescence quenching of Antarctic lichens (e.g. Adamson *et al.* 1990) largely ignored hydration state, which may well have obscured otherwise meaningful comparisons between lichens from different sites. Other investigations of the F_v/F_m ratio have yielded much more detailed information on the state of the photosystem in relation to WC, particularly since the advent of modulated fluorescence systems allowed the determination of photochemical and non-photochemical quenching parameters (e.g. Jensen 1994, Lange *et al.* 1989, Manrique *et al.* 1993).

Conventional IRGA studies of field photosynthetic activity in polar lichens have had to concentrate on either short-term monitoring or few species and few replicates (Kappen *et al.* 1988, Kappen 1989). A portable modulated fluorometer can be used to estimate photosynthetic activity in several species, complete with replicates, in several microsites for a long period because the measurements are rapid and require little preparation. This technique has allowed measurements of natural patterns of photosynthesis in the Antarctic crustose lichen *Buellia frigida* (Schroeter *et al.* 1992).

Continuous monitoring of photosynthetic activity is possible with a specially constructed modulated fluorometer. Schroeter *et al.* (1991*b*) showed that such a system is capable of operating in Antarctica for a period of several days without being attended. This is a major breakthrough, despite the fact that the signal really only provides an indication of metabolic activity rather than a measurement of net carbon assimilation. Such a system used to monitor, say, lichens under a blanket of snow from the onset of spring, would provide useful data on the periods of photosynthetic activity in this situation, which is of considerable importance in the overall annual productivity of these lichens.

Most of the lichen species in continental Antarctica are either crustose or squamulose (Longton 1988), and have usually been avoided in photosynthetic studies. This has mostly been due to the adherence of the thallus to the substratum and the difficulty in estimating WC, as well as the very low assimilation rates of most crustose species. The natural tendency, therefore, is to use several thalli in an IRGA chamber to provide measurable rates of carbon assimilation. In the most extreme habitats, crustose and squamulose lichens are important microhabitats for invertebrates, fungi and microorganisms and, therefore, gas exchange results of large areas will actually be the carbon exchange of a community. Many crustose lichens are tiny, and others show marked zonation, with decaying central tissue and actively growing margins. Modulated fluorescence is likely to provide more information on these situations which are difficult to impossible to study with conventional IRGA techniques, especially in the field, due to low rates and significant heterogeneity.

Vegetation communities in Antarctica are often very simple structurally, with one species dominating small to large patches of substratum (Smith 1988*a*, 1990, Melick *et al.* 1994). The investigation of photosynthetic activity in these stands by IRGA techniques is not difficult, since any results can be attributed to the particular species unambiguously. However, there are many areas, especially in the Windmill Islands region, where species occur intermingled. This is most evident in the dominant species where *Usnea sphacelata* often occurs with *Buellia soredians* growing at its base and *Pseudephebe minuscula* is often associated with *Umbilicaria decussata* (Smith 1988*b*,

Melick *et al.* 1994, see also Ch. 3). In these situations, the use of conventional IRGA chambers or porometer heads will not provide species-specific data since more than one species may occur in a particular sample. The area involved in a fluorescence measurement with an instrument such as the PAM-2000 with fibre-optics attachment is usually 0.3 - 0.5 cm^2 so individual thalli can be investigated. This allows the separation of species growing intermingled so that different species responses can be investigated under identical natural conditions.

4.6 Intrathalline Variation in Photosynthesis

The implications of non-uniform photosynthetic activity within a single lichen thallus are great and have been discussed by Kershaw (1985). It has been shown that thallus size affects lichen gas exchange rates in some species (Larson 1984), and there is considerable intrathalline variation of both photosynthetic rates and water relations (Larson 1983, Nash *et al.* 1980). This causes problems for the study of lichen growth, since a single figure of CO_2 exchange for a thallus is very much an oversimplification when photosynthesis and water relations are non-uniform. At any one time, various parts of a thallus may be carbon sources, others carbon sinks and still others metabolically inactive. Earlier studies of intrathalline variation in metabolic activity have utilised tedious measurements of the uptake of radioactive CO_2, or studied thalli which have been cut into small pieces. Both of these procedures are destructive and unsuitable for field studies. The rapid nature of fluorescence measurement and the small measuring area enable the quantification of patterns within individual thalli in both the laboratory and field.

Photochemical quantum yield of a large thallus of *Buellia frigida* from Granite Harbour, continental Antarctica (77° 00' S 162° 35' E), was investigated during dehydration using a grid of 70 measurement points scattered over the thallus (Schroeter *et al.* 1992). Thallus margins became photosynthetically inactive before the thallus centre, related to dehydration patterns within the thallus, but the pattern of dehydration was not radially uniform, further complicating the issue.

4.7 Problems with Dark Adaptation of Samples

While measurements of the Kautsky curve undoubtedly supply much information on the state of the photosystem and are an effective

diagnostic probe of phenomena such as photoinhibition (Ögren 1991), there remain problems with its use in lichen investigations. Interpretations of the curve, and of the F_v/F_m ratio in particular, rely on the assumption that the photosynthetic apparatus is completely dark-adapted when investigated. The period of darkness required for dark adaptation of leaves is usually considered 15 - 30 minutes (Bolhàr-Nordenkampf *et al.* 1989). When studying lichens in the laboratory, the conditions which determine the temperature and hydration of the lichen thallus may be controlled precisely and therefore changes in these parameters during the period of dark adaptation can be easily avoided. In the field, however, the microenvironment of the lichen thallus may be very different to general ambient conditions, particularly in Antarctica. The WC of Antarctic lichens in the field is dependent upon thallus temperature and microsite RH, as well as the presence of snow or melt water run-off (see Ch. 5). Many Antarctic lichens have darkly pigmented cortical layers and their thallus temperatures may be much higher than their surrounding atmosphere because of absorption of solar radiation (see below). Figure 4.4 shows microclimatic data from lichen dominated vegetation on Clark Peninsula. During the day in early summer, thalli of *Umbilicaria decussata* near Casey Station are frequently more than 30K warmer than ambient. It is likely, therefore, that shading a lichen *in situ* for up to 30 minutes will alter its thallus temperature and WC. Since carbon assimilation rates are dependent upon these variables, allowing a lichen thallus to dark-adapt in the field may alter its photosynthetic state. It must be pointed out, however, that most Antarctic lichens are not photosynthetically active when they are very warm. This is not always the case, however, as demonstrated in Ch. 5. Therefore, care should be taken when using F_v/F_m ratios as sole indicators of photosynthetic efficiency of Antarctic lichens in the field. Fluorescence induction curves, which involve F_o and F_m determination, require dark-adapted samples which are then exposed to actinic light of a particular intensity while q_N and q_P are monitored by regular saturation pulses (Schreiber *et al.* 1986). These too, although very useful for studies of environmental stresses to the photosynthetic processes in the controlled conditions of the laboratory (Schäfer and Björkman 1989), and in less severe climates, must be employed carefully in Antarctic field investigations. Problems may arise not only from the period of dark-adaptation, but also from changes in thallus temperature and WC during the period of fluorescence

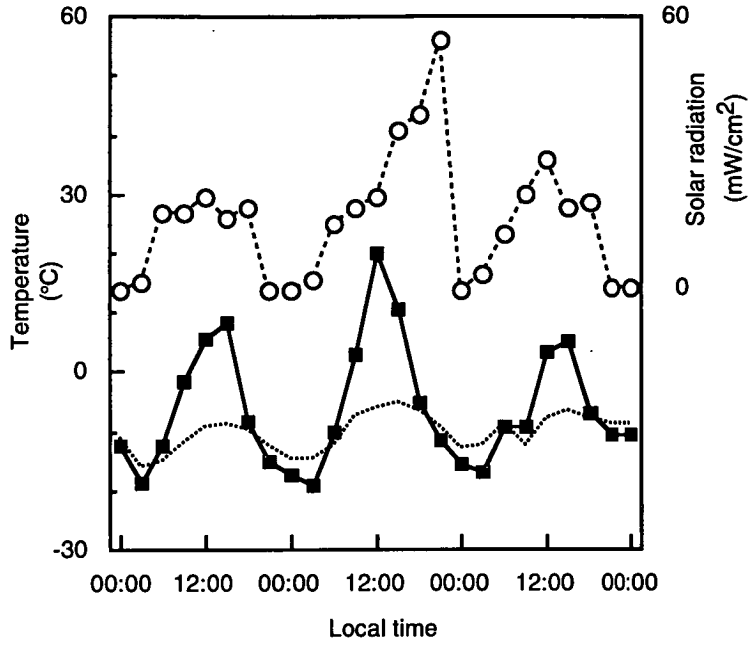

Figure 4.4 The relationship between thallus temperature of *Umbilicaria decussata* (open squares), ambient temperature (dotted line) and solar radiation (open circles) on a north facing slope on Clark Peninsula for 3 days in late October.

analysis, which could confuse interpretations of the induction curves. The same is true for the investigation of q_N relaxation kinetics.

As a consequence of these considerations, fluorescence parameters which do not require F_o determination, and therefore can be measured in light-adapted plants, are probably the most suitable for field measurements in Antarctica. Of these the most useful is the photochemical quantum yield parameter, ϕ_{PSII}, which is determined as $\Delta F/F'_m$ (Genty *et al.* 1989) and has been shown to be an accurate predictor of photosynthetic assimilation rates under diverse conditions (Edwards and Baker 1993).

4.8 Thallus temperature and photosynthesis.

Antarctic lichens have long been known to maintain positive carbon assimilation down to temperatures as low as -18.5°C (Lange & Kappen 1972). The temperature optimum for photosynthesis in continental Antarctic lichens varies with PPFD, and is generally close to freezing point at the low light conditions typical in lichen habitats (Kappen *et al.* 1995). With increasing PPFD, the temperature optimum of photosynthesis also increases in most species studied so far (Kappen *et*

al. 1995). Net assimilation of CO_2 has been observed in very cold thalli (-10°C) at high light conditions (922 $\mu mol.m^{-2}.s^{-1}$ PPFD), although at about 10% of the rate at +1°C (Schroeter *et al.* 1994).

The time generally considered to be the growth period for continental Antarctic lichens, late October until early March (Kappen *et al.* 1991), is also the time of highest thallus temperatures, although when the lichen thalli are wet, temperatures are often depressed. Schroeter (1991, cited in Kappen 1993) showed that lichens from Maritime Antarctica exhibited thallus temperatures close to their photosynthetic optimum when thalli were wet. This also is reported to occur at continental Antarctic sites when lichens are moist (Kappen 1985). This is due to the fact that lichens in continental Antarctica mostly rely on snow to provide the moisture necessary for photosynthesis, and this is obtained either from snow showers, when light levels are generally low due to cloud cover, or when lichens are covered by snow (Kappen 1993).

The measurement of lichen thallus WC is, itself, very problematic. As yet the only reliable method is gravimetric and involves weighing the fresh thallus followed by desiccation and reweighing. Several other methods have been proposed, including an electrical resistance method (Coxson 1991) and thermocouple psychrometry (Beckett 1995), but none have yet proved reliable in the extreme conditions of Antarctica.

Chapter 5

Photosynthetic Activity of Antarctic Lichens in the field and laboratory

5.1 Introduction

Antarctic lichens exist for long periods in a desiccated state. Free water is scarce in most localities and is only present intermittently for short periods. Lichens with green algal photobionts have been shown to absorb water from humid air alone and to maintain photosynthetic activity at very low temperatures (Kappen 1989, Lange *et al.* 1989). Over the last two decades there have appeared a plethora of papers dealing with lichen photosynthesis and its interaction with thallus hydration (e.g. Lange 1969, Kershaw 1971, Lange and Matthes 1981, Nash *et al.* 1990). Most of these deal with total carbon exchange of the symbiosis, although in more recent years studies of photosystem II fluorescence have provided information on the state of the photobionts (e.g. Jensen and Feige 1991). Fluorescence studies on lichens have been predominantly laboratory based (e.g. Lange *et al.* 1989). Recently, Schroeter *et al.* (1992) studied the field photosynthetic activity of antarctic lichens using the Walz PAM-2000, a portable modulated fluorescence system (see Ch. 4).

During the summer of 1992-93 I used a PAM-2000 modulated fluorescence system to investigate the field photosynthetic activity of three macrolichens in the vicinity of Casey Station, with respect to thallus WC, microclimatic conditions and time of day. In order to determine the effects of hydration due to snowfall, observations were made on days without precipitation as well as during and immediately after snow showers. The first was a summer day with no precipitation, and the second and third were the next occasions on which snow showers occurred. The field observations were supported by laboratory experiments concerning the short-term responses of lichen photosynthesis and water content to atmospheric humidity and artificial moistening.

All measurements were made on lichens within a flat, relatively uniform area 20 m x 40 m in size, approximately 100 m south of a field hut on Bailey Peninsula. The area was chosen for proximity to both Casey station and the field hut and because the site exhibited

reasonably uniform vegetation and microclimatic conditions. During the summer months the area is generally free from snow except during and immediately after snow showers. In the winter the site is usually covered with approximately 0.5m of packed snow.

5.2 Material and methods

5.2.1 Microclimate measurements

During the period of field measurements the thallus temperature of each of the three lichen species was monitored using Grant miniature thermocouple probes inserted into two randomly selected thalli for each species. Microclimate relative humidity was measured at thallus level using two Vaisala humidity probes subjectively placed in areas thought to be representative of the study site. Relative humidities and thallus temperatures were logged every hour by a Grant Squirrel SQ16 data logger. Photosynthetic photon flux density (PPFD) was measured by two LiCor LI-190SB quantum sensors logged with an LI-1000 data logger using a 60 s integration period and recording maximum, minimum and mean PPFD every 30 min. Gross climatic observations were made at Casey station by Australian Bureau of Meteorology observers every three hours.

5.2.2 Field measurements of fluorescence and thallus hydration

The Walz PAM-2000 portable modulated fluorescence system was used exactly according to manufacturer's instructions and as discussed in Chapter 4. The fibre-optic head was mounted in the distance clip which maintained an angle of 60° between fibre-optic cable and sample at a distance of approximately 4 mm, care always being taken not to shade the sample. The PAM-2000 was operated through a Poqet notebook computer which also stored all data and calculated fluorescence parameters.

Photochemical quantum yield of photosystem II was estimated for each species in a minimum of three replicate thalli in each of three randomly selected sites within the study area. Each measurement took approximately five seconds. The photochemical quantum yield was calculated as $\Delta F/F'_m$ for each individual measurement and then averaged over the replicate thalli for each species at each site.

Field measurements were made on three separate occasions; an early summer day with no precipitation, little wind and high PPFD levels

and after the next two occurrences of snow showers. On the first occasion measurements were made from 13 30 h (local time) 17 December 1992 to 04 00 h 18 December 1992. The second monitoring period was after a few hours of moderate snow fall with measurements being made every four hours from 16 00 h 23 December 1992 until 20 00 h 24 December 1992. The third occasion was a day with morning snow showers which cleared and the day brightened to high light intensity, measurements being made every two hours from 10 00 h until 18 00 h 8 January 1993. On both the first and third of these occasions (17 and 18 December and 8 January) all three species were investigated while on 23 and 24 December only *Pseudephebe minuscula* and *Umbilicaria decussata* were studied.

Specimens were collected for thallus water content estimation from the exact sites of fluorescence measurements. Thalli were removed from the substratum by severing the attachment with a razor blade as close as possible to the rock surface. Upon collection any adherent snow was removed by shaking. Thalli were measured for fresh weight on a Sartorius precision electronic balance in the nearby field hut, dried for at least 24 h in a laboratory oven at 70°C and reweighed. Thallus water content was calculated as a percentage of thallus dry weight.

5.2.3 Photochemical quantum yield and electron transport rates under controlled conditions in the laboratory.

Twelve large thalli of *Umbilicaria decussata* were collected intact from a north-facing rock face near the study area and placed in a growth cabinet in the laboratory. The lichens were permitted to acclimate for three days in the cabinet with a daytime PPFD of c. 70 $\mu mol\ m^{-2}\ s^{-1}$ in a 12:12h day/night cycle at 5°C. These conditions resulted in a thallus temperature of approximately 10°C during the day, which, along with the day length, is considered fairly representative of an early-summer day. All thalli were weighed on a Sartorius precision electronic balance at the beginning of the observation period. The individual thalli were then placed under 8 cm diameter plastic chambers in the presence of soaked filter paper to provide a humid atmosphere. The RH of these miniature chambers was usually close to 90% (Vaisala humidity probe). Three randomly selected thalli were then measured for fluorescence and thallus weight at 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 6, 9, 12, 18, 21, 24, 27, 30, 33, 36, 42, 45, 48 and 51 h. Thalli were then misted

with melt water and allowed to dehydrate gradually in the growth cabinet in an atmosphere of about 70% RH, which is approximately the median microclimate humidity during the summer months. Every 20 minutes for 500 minutes three thalli were randomly selected and measured for fluorescence and thallus weight. The lichens were illuminated at 70 μmol m^{-2} s^{-1} PPFD throughout this period.

Fluorescence measurements were made in the laboratory using the leaf clip connected to the PAM-2000 (see Ch. 4). The leaf clip is similar to those used in porometers and holds the leaf/thallus clamped between two perspex rings. The leaf clip monitored PPFD at the thallus surface with a micro-quantum sensor and thallus temperature with a NiCr-Ni miniature thermocouple pressed to the thallus undersurface. The leaf-clip was connected to the PAM-2000 via an RS-232 cable and temperature and PPFD measurements were automatically incorporated into every fluorescence measurement.

The simultaneous measurement of photochemical quantum yield and PPFD at the same point allow the calculation of apparent photosynthetic electron transport rate (ETR), which is merely the product of the two expressed in arbitrary, although relative, terms. Calculation of the actual photosynthetic electron transport rate requires the absorption coefficient of the photosynthetic surface, which in lichens is problematic due to variation between and within thalli and species. Since the ETR measurements were restricted to a standardised sample from one species the reflectivity of the thalli was ignored. The ETR values were normalised to 10°C, to remove any variations caused by slight differences in thallus temperature, by dividing the ETR value by the thallus temperature and multiplying by ten.

The ETR of some large *Umbilicaria decussata* thalli in the field was also measured on 8 January 1993 immediately after the morning snow showers and four hours later. The measurements were made in exactly the same manner as for the laboratory studies. It was possible to do more than one measurement on some of the larger thalli to gain some indication of the intrathalline variability of ETR. Each thallus was collected immediately after measurement to assess thallus water content as described above.

5.3 Results

5.3.1 December 17 and 18, 1993

The microclimatic variables for the measuring period are detailed in Table 5.1. The relative humidity was highest during the "night" which was also the time of lowest ambient temperature and PPFD. During the measuring period the PPFD reached a maximum of around 900 μmol m^{-2} s^{-1} but fell to quite low levels during the evening (7 μmol m^{-2} s^{-1}). By early morning the PPFD had returned to quite bright conditions (365 μmol m^{-2} s^{-1} at 06 00 h). Thallus temperatures (Table 5.1) were generally similar between the species and were lowest in the early hours of the morning. None of the lichens showed any measurable photosynthetic activity during the measuring period of 17 and 18 December 1992 (Table 5.2). Thalli of *Usnea sphacelata* were uniformly desiccated throughout the period (Table 5.2). The water content of the other two species was more variable, depending upon site and species (Table 5.2). *Pseudephebe minuscula* reached greatest levels of hydration during the evening, when the relative humidity was highest (Table 5.2), whereas *Umbilicaria decussata* thalli showed highest level of thallus hydration earlier in the day, when it was both warmer and brighter.

5.3.2 December 23 and 24, 1992

Figure 5.1 shows the microclimatic variables for the measuring period on 23 and 24 December 1992 as well as thallus temperatures, water content and photochemical quantum yield for *Pseudephebe minuscula* and *Umbilicaria decussata*. 1.0 mm of snow (rainfall equivalent) fell during the 24 hours to 11 00 h 23 December 1992 and trace amounts fell on 24 December. The plots of photochemical quantum yield and water content versus time (Figure 5.1d-g) show the relationship in the field between the two physiological variables at Sites A and B. Both *Pseudephebe minuscula* and *Umbilicaria decussata* were photosynthetically active for most of the measuring period. Thallus water contents were variable depending upon site, species and time. At Sites A and B, *Pseudephebe minuscula* had a higher thallus water content than *Umbilicaria decussata* although the trends of hydration with time were similar between the species. Photochemical quantum yield differed markedly according to both site and species, but in

TABLE 5.1 *Microclimate variables in study site and thallus temperatures during 17 and 18 December 1992 for two random thalli (a and b) of* Pseudephebe minuscula, Umbilicaria decussata *and* Usnea sphacelata.

	Thallus temperature (°C)						Ambient	PAR	RH (%)	
	Pseudephebe		*Umbilicaria*		*Usnea*		Temp.	($\mu mol.m^{-2}.s^{-1}$)		
Time	a	b	a	b	a	b	(°C)		a	b
13 00	8.8	9.6	8.4	8.4	9.2	9.2	2.09	521	41	45
14 00	7.6	9.6	9.6	10.0	11.2	10.4			38	51
15 00	10.0	10.0	9.6	8.4	10.4	10.0	2.91	900	38	51
16 00	7.6	9.2	8.4	7.6	8.4	8.8			51	57
17 00	8.4	12.8	10.8	9.6	10.8	11.6			38	44
18 00	7.2	6.8	8.8	7.6	8.8	9.2	1.18	250	45	53
19 00	6.4	6.4	7.6	6.4	7.6	8.0			49	54
20 00	4.4	4.8	6.0	4.8	6.0	6.0			59	58
21 00	2.4	2.0	4.0	3.2	4.0	3.6	0.00	47	70	67
22 00	0.4	0.4	2.4	2.0	2.4	2.4			76	71
23 00	-0.8	-0.4	1.2	0.8	0.8	0.8			71	65
00 00	-2.0	-1.2	0.4	0.0	0.0	0.0	-0.36	7	66	62
01 00	-2.4	-1.2	0.0	-0.4	-0.4	-0.4			64	59
02 00	-3.2	-1.2	-0.4	-0.8	-1.2	-0.8			70	59
03 00	-4.8	-2.4	-1.6	-2.0	-2.4	-2.0	-1.80	74	74	63
04 00	-5.2	-3.6	-2.0	-2.4	-2.4	-2.4			68	64
05 00	-3.6	-3.6	-0.4	-0.8	-0.8	0.0			58	60
06 00	-1.6	-0.8	0.8	1.2	1.6	2.0	-0.18	365	52	56
07 00	0.0	0.4	2.4	2.8	3.6	3.2			45	51
08 00	3.2	3.6	4.8	4.4	8.0	6.0			40	48
09 00	7.6	7.2	10.0	10.0	16.0	12.0	2.36	1035	25	42

TABLE 5.2 Thallus water contents (WC) as % DW for the three lichen species at each of three sites (A, B and C) during 17 and 18 December 1992.

Time	Site	*Pseudephebe*	*Umbilicaria*	*Usnea*
13 40	A	40	77	23
13 40	B	60	124	35
13 40	C	45	50	31
15 40	A	44	86	35
15 40	B	28	47	32
15 40	C	56	115	26
17 40	A	86	76	31
17 40	B	35	42	27
17 40	C	56	59	35
19 40	A	47	44	29
19 40	B	51	41	28
19 40	C	114	52	22
21 40	A	73	45	35
21 40	B	34	51	33
21 40	C	139	49	33
23 40	A	63	35	31
23 40	B	28	36	27
23 40	C	52	60	27
0140	A	39	48	29
0140	B	29	39	28
0140	C	36	32	26

general $\Delta F/F'm$ values were lowest when thallus water contents were either very high or very low. Photochemical quantum yield at Site C was virtually identical for both species (Figure 5.1h) as were the trends in thallus hydration (Figure 5.1i).

Site variation in the temporal response of photochemical quantum yield within a species was quite marked, especially in *Pseudephebe minuscula,* as were thallus water contents. At both Sites A and B the $\Delta F/F'm$ values were high between 20 00 h and 04 00 h despite quite variable levels of thallus hydration. At Site C the photochemical quantum yield of *Pseudephebe minuscula* was also high at 20 00 h and 00 00 h but at 04 00 h, a time of very low thallus water content, $\Delta F/F'm$ was zero. In *Umbilicaria decussata* from Sites A and B both thallus water contents and photochemical quantum yield were less variable

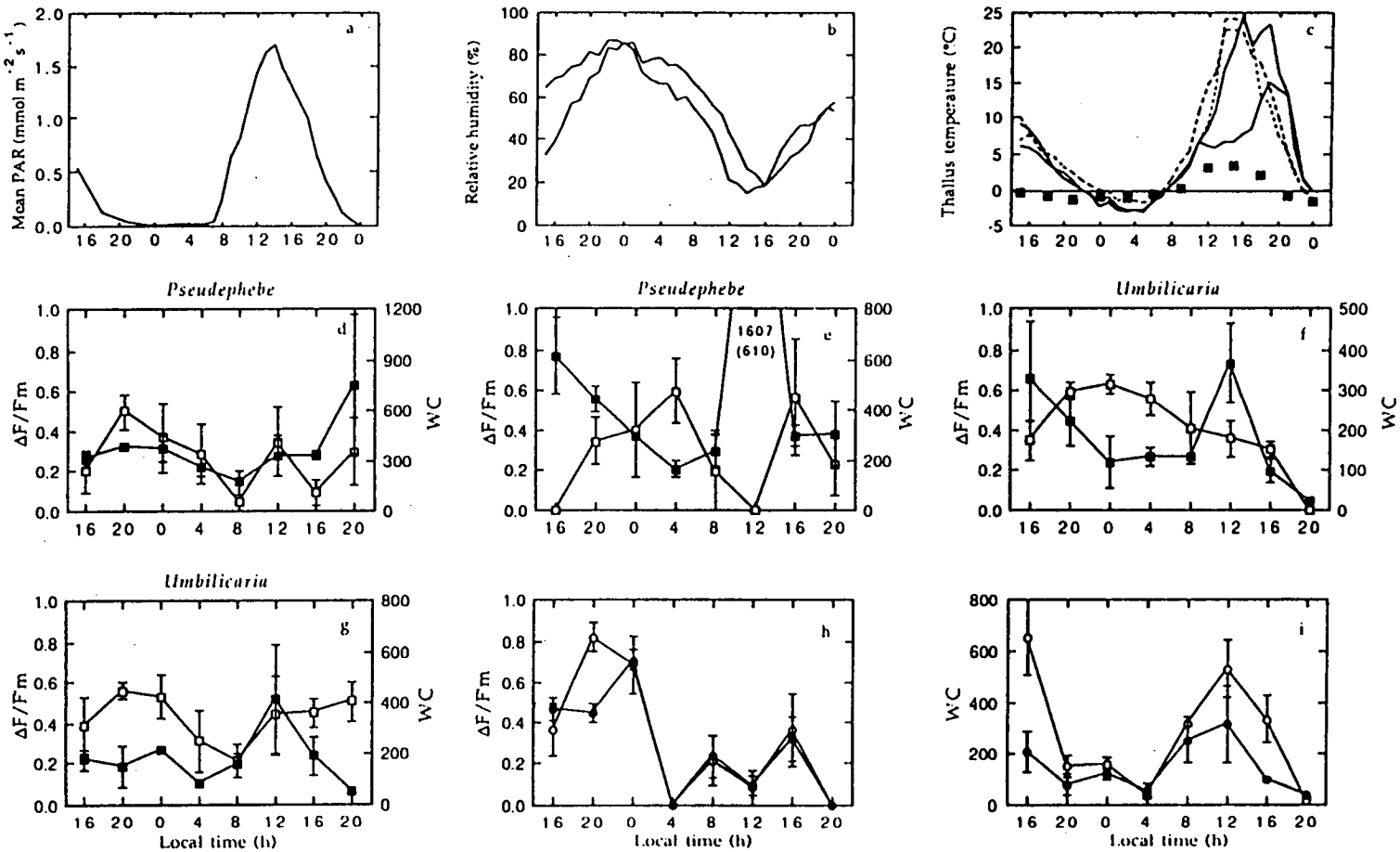

Figure 5.1 (a-c) Microclimate variables in the study site, 23 & 24 December 1992. (a) Mean PAR. (b) RH in two sites. (c) Thallus temperature in *Pseudephebe* (dashed line) and *Umbilicaria* (solid line) and ambient temperature (filled squares). (d-g) ΔF/F'm (open squares) and thallus WC as % dry weight (filled squares) during 23 & 24 December 1992 at Sites A (d, f) and B (e, g). (h, i) ΔF/F'm (h) and thallus WC (i) for *Pseudephebe* (open circles) and *Umbilicaria* (filled circles) from Site C. The vertical lines (d-i) are ±SE. The number at 1200 h (e) is the mean thallus WC with SE in parentheses.

than for *Pseudephebe minuscula* from the same site. Quantum yields of *Umbilicaria decussata* tended to be highest at 20 00 h and 00 00 h at all sites. The time of highest water content for both species was at 12 00 h on 24 December 1992, including an extremely high thallus water content for *Pseudephebe minuscula* from Site B. This was a time of extremely high PPFD (maximum reading 2430 $\mu mol\ m^{-2}\ s^{-1}$) and relatively high ambient temperature (+3°C) which combined to cause rapid melting of accumulated snow and consequently thalli were saturated with melt water. A significant depression of photochemical quantum yield was associated with this phenomenon in *Pseudephebe minuscula* from Sites B and C (Figure 5.1e, h). The low value for thallus water content in both species at all sites at around 04 00 h 24 December 1992 reflects the lowest thallus temperatures in the sample period coupled with low ambient temperature and low PPFD. At Site C this is associated with a large drop in the photosynthetic activity of both species.

5.3.3 January 8, 1993

Microclimate variables for 8 January 1993 are presented in Figure 5.2 with thallus temperatures and photochemical quantum yield for all three species. 1.4 mm of snow fell in the 24 hours until 11 00 h 8 January 1993. Thallus water contents for the period are shown in Table 5.3 although sample losses resulted in an incomplete set of thallus water contents. The patterns of photochemical quantum yield for 8 January 1993 were similar between sites for each species (Figure 5.2d-f). At 12 00 h, which was a time of high PPFD, $\Delta F/F'm$ was significantly depressed in *Pseudephebe minuscula* but not in *Umbilicaria decussata*. Thallus water contents for *Pseudephebe minuscula* were very different between the sites at this time, although still quite high. The photochemical quantum yield of *Usnea sphacelata* showed a gradual decrease from maximal values immediately after snowfall to zero values six hours later as the thalli dried out in all sites. All species were photosynthetically inactive by the early evening. The $\Delta F/F'm$ values for both *Pseudephebe minuscula* and *Umbilicaria decussata* were generally lower than for similarly hydrated specimens on 23 and 24 December 1992.

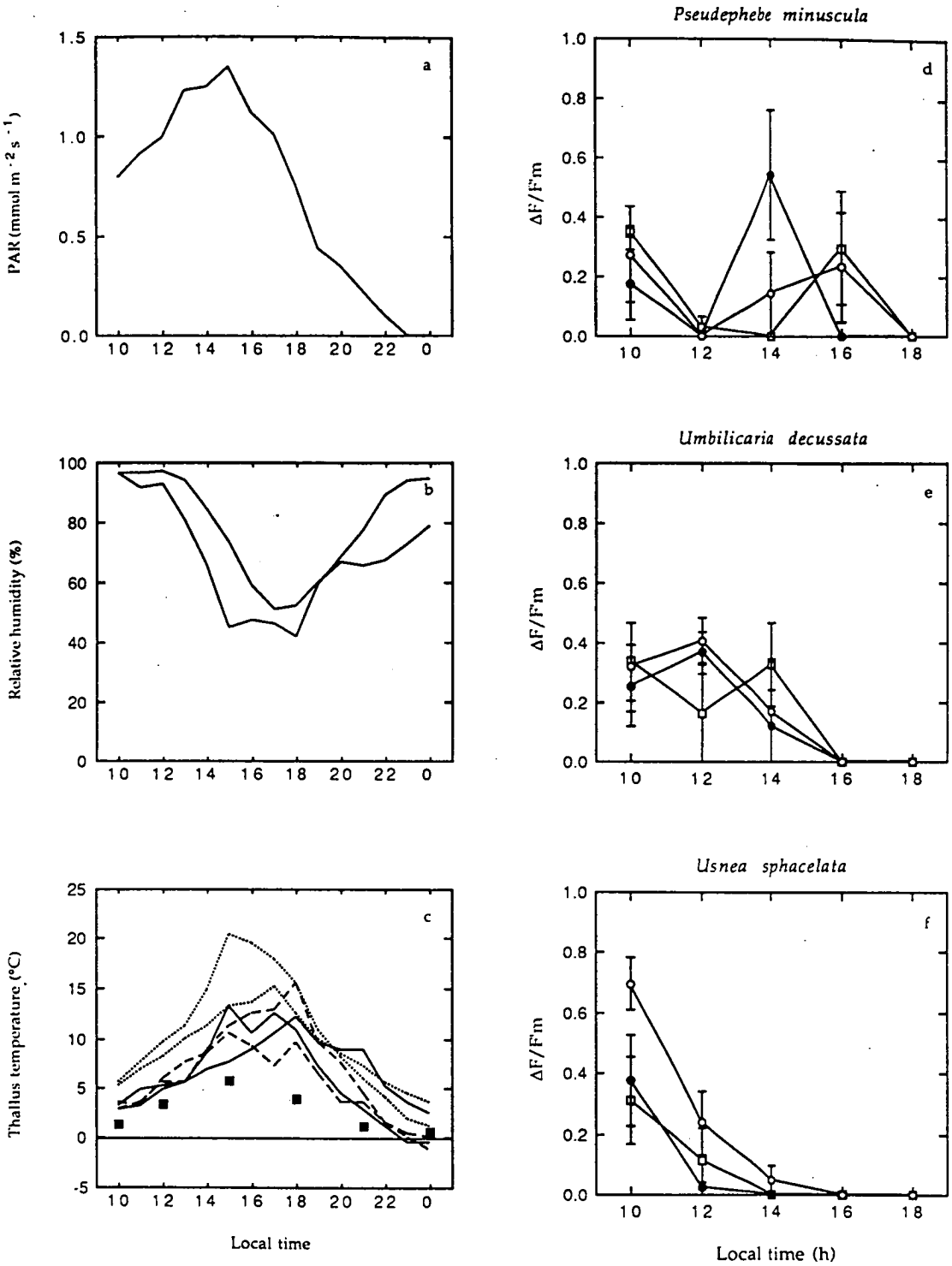

Figure 5.2 (a-c) Microclimate variables in the study site, 8 January 1993. (a) Mean PAR. (b) RH in two sites. (c) Thallus temperature in two random thalli of *Pseudephebe* (dotted line), *Umbilicaria* (solid line) and *Usnea* (dashed line) and ambient temperature (filled squares). (d-f) ΔF/F'm at Sites A (open squares), B (filled circles) and C (open circles) during 8 January 1993. Vertical lines (d-f) are ±SE.

TABLE 5.3 *Thallus water contents (WC) as %DW (±SE) for* Pseudephebe minuscula, Umbilicaria decussata *and* Usnea sphacelata *at three sites (A, B and C) on 8 January 1993.*

Pseudephebe minuscula				*Umbilicaria decussata*				*Usnea sphacelata*			
Time	Site	WC		Time	Site	WC		Time	Site	WC	
12 00	A	325	±5	12 00	A	261	±5	12 00	A	101	±12
12 00	B	1611	±789	12 00	B	403	±17	12 00	B	263	±87
12 00	C	778	±161	12 00	C	310	±2	12 00	C	107	±35
16 00	A	221	±45	14 00	A	40	±16	14 00	A	33	±4
16 00	B	240	±111	14 00	B	51	±5	14 00	B	56	±3
16 00	C	242	±27	14 00	C	44	±2	14 00	C	28	±1
18 00	A	60	±16								
18 00	B	-	-								
18 00	C	65	±11								

5.3.4 Photochemical quantum yield and electron transport rates under controlled conditions in the laboratory.

Thalli of *Umbilicaria decussata* were very dry and brittle when first placed in the growth cabinet. Actual thallus water contents ranged between 13.5% and 18.5% dry weight. All thalli absorbed water vapour directly from the humid atmosphere reaching a mean water content of c. 50% dry weight after approximately 20 h after which there was no appreciable water uptake (Figure 5.3a). At no time in this period was any lichen measurably photosynthetically active.

When thalli were sprayed with melt water they became supple and appeared fully hydrated (maximum thallus water content 245% dry weight) and were photosynthetically active by the time readings could be taken (after about 2 min). The lichens then began to dehydrate reaching thallus water contents as low as 31.5% dry weight by 500 min (Figure 5.3b). Figure 5.3c shows the relationship between ETR and thallus water content for the experiment at 10°C and 70 μmol m^{-2} s^{-1} PPFD. The curve shows a peak in photosynthetic electron transport rate at thallus water contents around 90% which is consistent with field responses shown in Figure 5.1 and 5.2.

Electron transport rates of *Umbilicaria decussata* in the field were variable even within a thallus (Table 5.4). All thalli measured immediately after the snow showers were photosynthetically active although not in every lobe. In these conditions, the field values of ETR were similar to those of thalli in the laboratory. Four hours later thalli from the same area were warmer and exposed to much brighter conditions. Thallus water contents were lower but still mostly within the range suitable for photosynthesis. Only one thallus was photosynthetically active at this time, yet this lichen had very high electron transport rates and was substantially cooler than the other thalli.

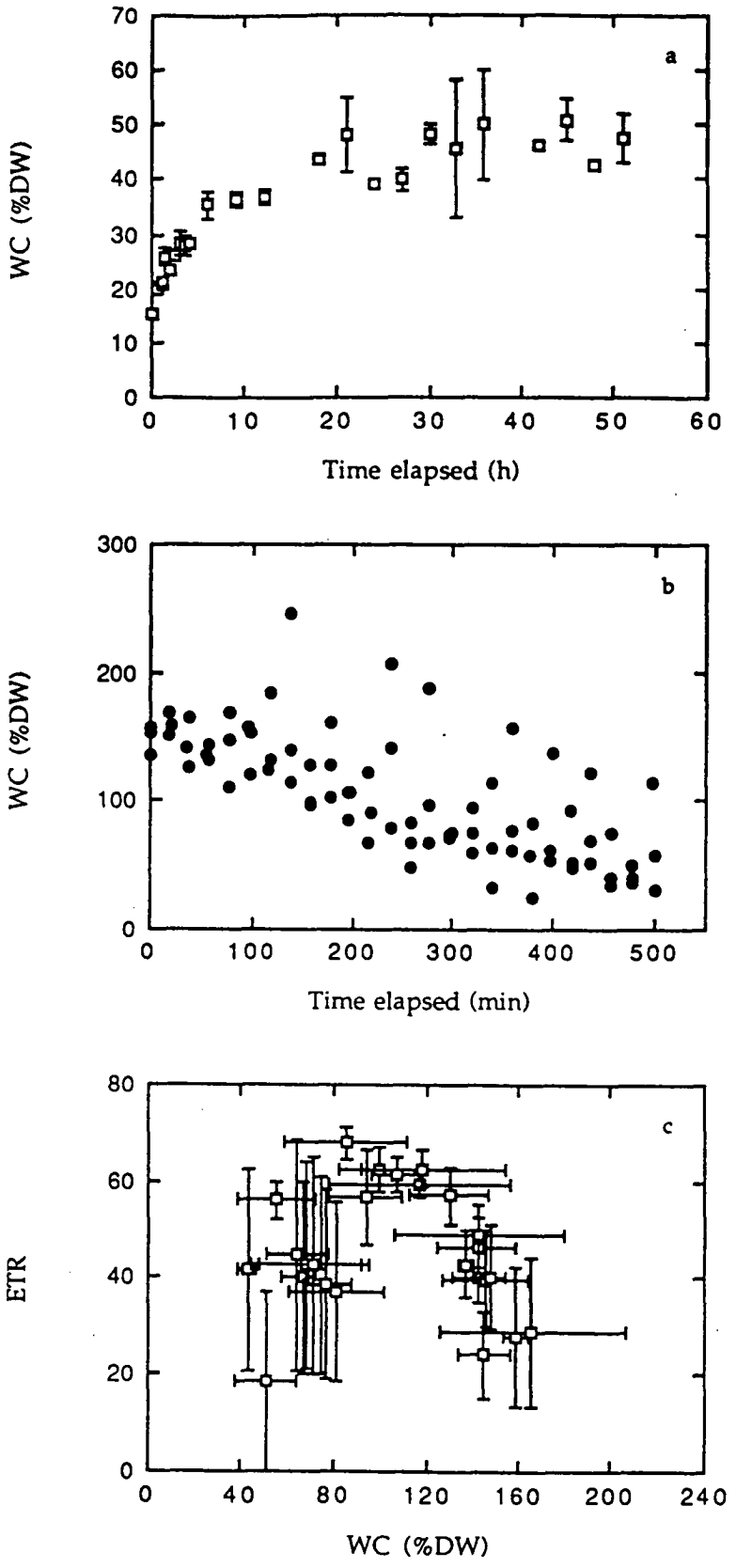

Figure 5.3 Water relations and photosynthetic activity of large *Umbilicaria decussata* thalli in controlled conditions of 5°C and 70 µmol m^{-2} s^{-1} PAR. (a) Mean thallus water content (WC) as a function of time of exposure to an atmosphere of 95% RH. Each point is the mean of three thalli. Vertical lines are ±SE. (b) Thallus WC as a funtion of time since misting with melt water. (c) Mean ETR as a function of thallus WC after being misted with melt water. Each point is the mean of three thalli. Both vertical and horizontal lines are ±SE.

TABLE 5.4 Physiological state of large *Umbilicaria decussata* thalli in the field on 8 January 1993. All variables except thallus water content were measured using the leaf-clip attachment on the PAM-2000. ETR is the apparent photosynthetic electron transfer rate expressed in arbitrary terms.

Time	Thallus	Temp. (°C)	PPFD ($\mu mol.m^{-2}.s^{-1}$)	$\Delta F/F'_m$	ETR	WC (%DW)
Immediately after snow showers						
11 00	A	9.8	132	0.185	24	393
11 02	A	10.2	67	0.292	20	
11 02	A	9.3	89	0.433	39	
11 03	A	9.8	89	0.282	25	
11 07	B	9.6	208	0.000	0	251
11 09	B	8.9	119	0.043	5	
11 11	C	8.8	146	0.356	52	612
11 12	C	8.5	123	0.111	14	
11 18	D	10.8	329	0.889	292	339
Four hours after snow showers						
14 50	E	22.2	806	0.000	0	161
14 51	E	22.8	806	0.000	0	
14 51	E	21.3	233	0.000	0	
14 57	F	18.0	767	0.000	0	88
14 58	G	15.0	760	0.913	694	53
14 58	G	16.5	753	0.909	684	
15 04	H	20.5	741	0.000	0	184
15 06	I	18.9	695	0.000	0	30

5.4 Discussion

Lichens show a marked relationship between thallus water content and carbon exchange (Lechowicz 1982). This usually takes the form of an optimum water content above and below which carbon assimilation rates decline. The effects of thallus moisture on CO_2 exchange in lichens have been well discussed by Harrisson *et al.* (1989) and Green *et al.* (1994). The study of lichen photosynthesis through CO_2 exchange is complicated not only by the varying diffusive resistance of the thallus at different water contents but also by the different contributions of photobiont photosynthesis, photobiont and mycobiont dark respiration and photobiont photorespiration. Gas exchange analysis can not differentiate these various contributions to apparent photosynthesis and studies of the isolated photobionts may

bear no resemblance to trends *in situ*, but direct estimation of the activity of photosystem II by fluorescence analysis may help to elucidate the situation at this level.

Dry lichens with green algal photobionts are able to reactivate photosynthesis by absorbing water vapour from the surrounding air (e.g. Kershaw 1985, Lange and Kilian 1985, Lange *et al.* 1986, 1989) while those with cyanobacterial photobionts are unable to do so (Lange *et al.* 1993b). There are no known continental antarctic lichens with cyanobacterial photobionts. Laboratory based studies by Lange and Kappen (1972) showed that several continental antarctic lichens reactivated photosynthesis when exposed to almost saturated air for more than 24 h. Long term measurements of the lichen microclimate in the Windmill Islands (see Ch. 3 and Ch. 6) reveal that microsite RH is seldom high for long periods except when lichens are covered by snow, therefore it is likely that all of the major macrolichens in the Windmill Islands rely almost exclusively on snow as a water source. This is supported by the field measurements of 17 and 18 December along with the laboratory result that thalli of *Umbilicaria decussata* were photosynthetically inactive even after 51 h exposure to 90% RH.

In the Windmill Islands region the areas with the greatest abundance of lichens are typically snow free from December until late February, or even longer in particularly warm summers (e.g. 1991-92), and areas of very late-lying snow are devoid of lichen growth (Melick *et al.* 1994, Ch. 7, see also Benedict 1990). Previous investigations of gas exchange of continental Antarctic lichens have concentrated on thalli in contact with snow (Kappen 1989, Kappen and Breuer 1991) or with thalli artificially wetted (Kappen *et al.* 1991). The discussions of Kappen *et al.* (1991) are based on thalli being covered by snow, however our observations over eight summers are that most vegetated areas are devoid of snow for the majority of the summer. Lichens are therefore exposed to dry atmospheric conditions for most of the summer. In addition, the number of summer days on which it snows is quite small hence the state of the lichens on 17 and 18 December is quite typical of the summer as a whole. It is therefore interesting that three of the dominant Antarctic macrolichens appear to be totally reliant on snow as a water source during the summer months, which is an important consideration when modelling photosynthesis (see Ch. 6).

After a period of snow fall provided free water to the lichens all three species started to photosynthesise. The diurnal courses of microenvironmental variables on 23 and 24 December caused thallus water contents to fluctuate considerably from well below to well above postulated optimal water contents for both *Pseudephebe minuscula* and *Umbilicaria decussata*. This may have contributed to the considerable variation in lichen photosynthetic activity over the course of the study. Lange (1980) showed that depression of photosynthesis by thallus saturation was more pronounced at higher thallus temperatures and thalli of all species studied here were always moistest at the times of highest thallus temperatures (see Figure 5.1) with *Pseudephebe minuscula* thalli reaching 24.0°C while experiencing 1750 μmol m^{-2} s^{-1} PPFD and having a mean water content of approximately 1600% dry weight. Any of these variables could have caused a depression of photosynthesis so together they resulted in total inhibition of photosynthesis. The diurnal changes in ΔF/F'm can be partly attributed to the changing levels of illumination over the study periods, but careful inspection of the data indicates that this is unlikely to be the overwhelming factor.

The interaction between thallus temperature, WC and photosynthetic activity is interesting with thalli being photosynthetically active at temperatures higher than reported elsewhere (Kappen 1993, see Ch. 4). The climatic conditions did result in unusual circumstances with snow falls being heavy enough to persist into later, much brighter conditions. Therefore the lichens were moist when exposed to high PPFD levels and therefore had high thallus temperatures. This is certainly a contributing factor to the day time decreases in ϕ_{PSII}. Direct evidence of the effect of high temperatures on photosynthetic activity is contained in Table 5.4 where *Umbilicaria decussata* thalli with moderate to high WC were photosynthetically inactive at temperatures of 18°C and above. These results support the arguments of Kappen (1985) who stated that Antarctic lichens with thallus temperatures much above 10°C would be photosynthetically inactive, and most lichens which were photosynthetically active would have thallus temperatures below 10°C.

Variation in photochemical quantum yield and thallus hydration was both site and species specific. At Sites A and B, *Umbilicaria decussata* and *Pseudephebe minuscula* showed definite distributional zonation

with the latter species occurring in the moister sites. This would account for higher levels of hydration in *Pseudephebe minuscula* in these sites but the difference in photochemical quantum yields is not as easily explained. While it is possible that there is some ecotypic difference in photosynthetic response, as is the case in *Nephroma arcticum* (Sonesson *et al.* 1992), varying thallus pigmentation may be partly responsible for the differences in $\Delta F/F'_m$. At Site C, however, the two species are codominant and thalli are fully intermingled. At this site the response of $\Delta F/F'_m$ during 23 and 24 December is virtually identical between the two species (Figure 5.1h). This indicates that the photochemical quantum yield of the species responds in a similar fashion to environmental variables. The thallus water content, however, is consistently higher for *Pseudephebe minuscula* in all sites while photochemical quantum yield is quite variable at Sites A and B. The results from Site C indicate that *Pseudephebe minuscula* maintains a higher thallus water content than *Umbilicaria decussata* from the same microhabitat while exhibiting similar levels of photosynthetic activity. It is possible that the measurements of thallus water content of *Pseudephebe minuscula* are an overestimate due to the presence of extracellular water trapped between the closely appressed filaments but this is unlikely to be responsible for the total observed difference. The variation in thallus water content between the species at a particular site and time is likely to be due to differences in thallus morphology.

Whichever factors led to the very low quantum yields of *Pseudephebe minuscula* at 12 00 h 8 January did not cause a similar reduction in those of *Umbilicaria decussata*. Together, the higher moisture levels and greater sensitivity to PPFD of *Pseudephebe minuscula* indicate that the species is probably most active when covered by snow, an observation which agrees with its local patterns of distribution and abundance. The reduction in photosynthetic activity of *Usnea sphacelata* at this time was probably due to dehydration since *Usnea sphacelata* dehydrated quickly and showed a rapid reduction in photosynthetic activity. This is supported by observations of uniformly low water contents on 17 and 18 December.

Variation in the levels of ETR within *Umbilicaria decussata* thalli under reasonably uniform conditions, as has been reported elsewhere (Larson 1983), may be due to uneven hydration within large thalli, as

occurs in *Buellia frigida* (Schroeter *et al.* 1992). Investigations of the interaction of ETR with thallus hydration, temperature and PPFD in small and large thalli are needed to clarify the situation.

Overall the trends of photosynthetic activity in the field agree with those from laboratory studies with highest levels of photochemical quantum yield occurring at intermediate water contents. Previous studies concentrated on lichens in direct contact with snow while this study investigated lichens exposed to the atmosphere. The results obtained contrast with those of the other studies by showing that macrolichens in equilibrium with the atmosphere are photosynthetically inactive for the large part of summer, relying upon snowfall to provide the necessary free water for the initiation of photosynthesis. Studies of the photosynthetic physiology of *Umbilicaria decussata* and *Pseudephebe minuscula* provide insight into the ecological patterns exhibited by these species. These studies show that hydrated lichens are often subjected to other stresses which may reduce photosynthetic efficiency. Brief snow showers are important as sources of water and lichens are able to photosynthesise even when illuminated by strong light. Experimental studies in controlled conditions are needed to determine the actual photosynthetic optima of *Pseudephebe minuscula* and to detail its apparent greater sensitivity to PPFD and higher thallus water compensation point. In addition, further studies of specific responses of *Umbilicaria decussata* photosynthesis to temperature and PPFD will also help explain the ecological patterns of this successful lichen.

Chapter 6

Lichen water uptake

6.1 Introduction

It has long been acknowledged that lichens with green algal photobionts can absorb sufficient water from a humid atmosphere to photosynthesise. Numerous observations from both the field (Lange *et al.* 1989) and laboratory (Lange and Killian 1985) have established that this trait is almost universal amongst green algal lichens but absent from cyanobacterial lichens. All known lichens from continental Antarctica have green algae as photobionts so one might expect that they will photosynthesise as a result of water uptake from the atmosphere. Measurements of antarctic lichen photosynthesis in the field have indicated that lichens in equilibrium with the atmosphere rarely photosynthesise as a result of water uptake from the air (Ch. 7, Gannutz 1967). These studies have been relatively short-term and have focussed on the dry summer period.

Measurement of the relative humidity of air has become commonplace and can be logged by automated instruments, consequently data for humidity in the microclimate of Antarctic lichens have been available for some time. The measurement of air temperature at the point of humidity measurement allows the calculation of the water potential of the air according to a derivation of Raoult's law such that

$$\Psi_{air} = -1.06\, T \log_{10} (100/RH) \qquad \text{Eqn. 6.1}$$

where Ψ_{air} is water potential of the air in MPa, T is temperature in kelvin and RH is relative humidity in percent.

A lichen will absorb water from a humid atmosphere when its water potential is lower than that of the air. Let us assume, as did Bölter *et al.* (1989), that a lichen in thermal equilibrium with an atmosphere of 80% RH can absorb sufficient water to re-initiate photosynthesis. Then we can calculate the lowest water potential of air from which lichen water uptake occurs, Ψ_{WU}, if we know the thallus temperature of the lichen. Thus, by substituting RH=80 into Eqn. 6.1, we have

$$\Psi_{WU} = -1.06\, T_l \log_{10}(100/80)$$
$$\Psi_{WU} = -0.103\, T_l \qquad \text{Eqn. 6.2}$$

where T_l is the thallus temperature of the lichen.

Thus, by measuring the temperature of the lichen thallus, the relative humidity of the air in the lichen microhabitat and the air temperature at the point of humidity determination, it is possible to compare the actual water potential of the air with that required to provide the lichen with water for photosynthesis, assuming that the lichen can photosynthesise when in equilibrium with 80%*RH*.

This chapter investigates lichen uptake of atmospheric water by modelling the atmospheric water potential and comparing it with that calculated as the minimum for lichen water uptake during late winter and early summer in the crest region of the knoll on Clark Peninsula (see Ch. 3).

6.2 Materials and Methods

All measurements were made on the crest region of a small rounded knoll on Clark Peninsula, Windmill Islands, continental Antarctica. The meso- and microclimate of the site are discussed in detail in Chapter 3. Lichen thallus temperatures were measured using miniature thermocouples which were logged every three hours by an Aanderaa 3010 automatic weather station. Microclimate humidity was measured with two Vaisala humidity probes and logged every 90 minutes using a Grant squirrel data logger. Humidity data were collected from mid-August until early January.

The actual Ψ_{air} was calculated according to Eqn. 6.1. The minimum water potential of the air necessary for lichen water uptake, Ψ_{WU}, was calculated according to Eqn. 6.2. Water vapour uptake was assumed to be sufficient to sustain lichen photosynthesis whenever Ψ_{air} was greater than Ψ_{WU}.

6.3 Results and Discussion

During the period of 21 August 1992 until 5 January 1993 the minimum air water potential for water vapour absorption by a lichen, Ψ_{WU}, varied from -23.7 MPa to -31.1 MPa, while the atmospheric water potential of the lichen microhabitat ranged from -5.82 MPa to below

-300 MPa. Figure 6.1 shows the range of Ψ_{air}, which is enormous compared to the range of Ψ_{WU} values. The lichen thallus temperatures during this period ranged from -42.8°C to 28.5°C and the ambient temperature in the microenvironment from -31.6°C to 6.6°C. For approximately 351h during this period, Ψ_{air} was greater than Ψ_{WU}, and therefore lichens in equilibrium with the atmosphere could absorb sufficient water to photosynthesise. This figure corresponds to 10.7% of the total time. The temporal distribution of this time during which photosynthesis from water vapour uptake was possible is given in Table 6.1.

From both Figure 6.1 and Table 6.1, it is obvious that November is the spring month when water uptake from the atmosphere is most likely, with conditions being favourable for approximately 37% of the month. This is undoubtedly linked to the onset of the summer thaw and the increase in atmospheric humidity due to the presence of free water in the lichen habitat. This was the the only extended period during which uptake of water vapour from the atmosphere was likely. Rare events further into summer, such as snow showers and fogs, provide periods of high atmospheric humidity, and such events are even more scarce during the winter. Therefore, over the spring as a whole, the potential for lichen photosynthesis as a result of water uptake directly from the atmosphere is low. It must be stressed, however, that this is the case for lichens exposed to the atmosphere. Lichens which are blanketed by snow during the winter and early summer would have a much greater potential for photosynthesis due to water vapour uptake since the air in the sub-nival space is considerably moister than that where snow is absent (Kappen, 1993). Water uptake directly from melting snow is also a very important source of water (Schroeter *et al.*, 1994) and late-lying snow may even lead to lichen death (Benedict, 1990). Lichens covered by snow are also sheltered from the extremes of temperature which occur during the spring and are completely protected from desiccating winds.

The extremely low values of Ψ_{air} during the winter are not surprising given the climate. Not only are air temperatures low, but the predominant southerly and easterly winds (Figure 3.2) mean that the air comes from across the Antarctic plateau, which is up to 4km high and extremely cold, resulting in what must be nearly the driest air on earth.

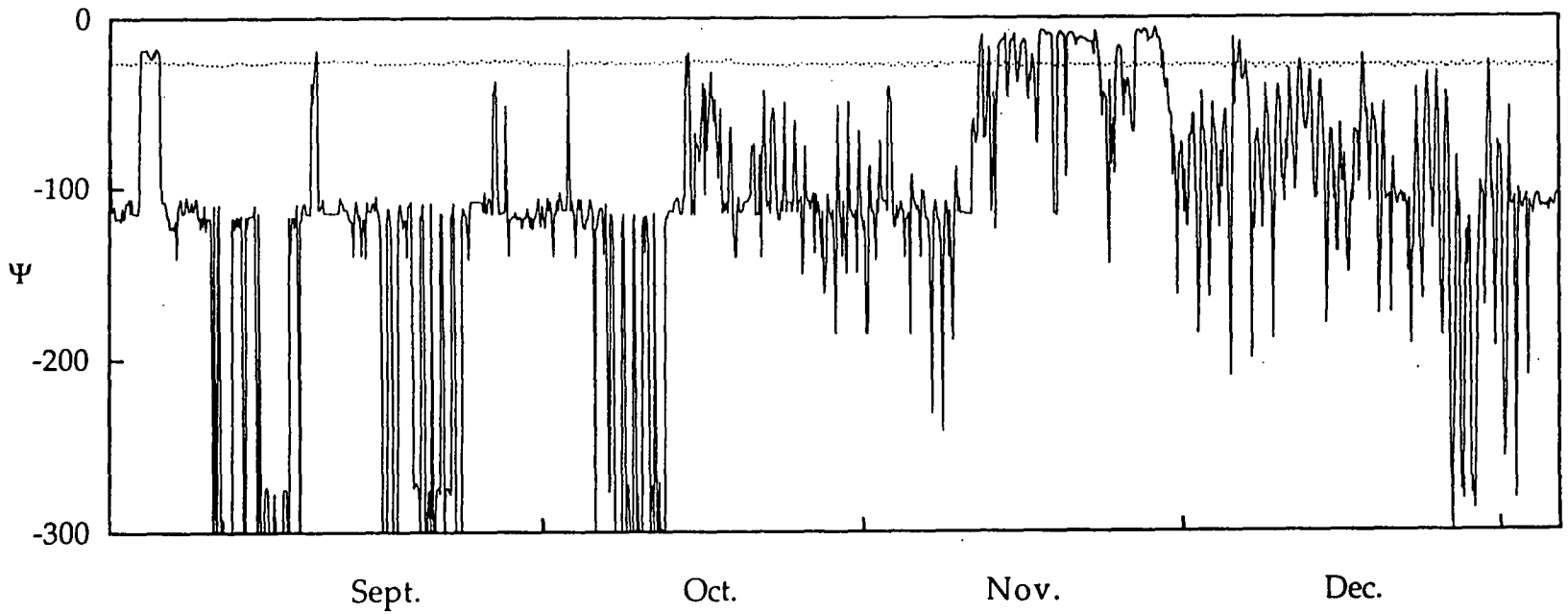

Figure 6.1 The time course of Ψ_{air} (solid line) and Ψ_{wu} (dotted line) during late winter and early summer of 1992. The abbrveiations are defined in text.

TABLE 6.1. Monthly potential for water vapour uptake by lichens on Clark Peninsula exposed to the atmosphere for the period of 21 August until 5 January using three critical RH values for water uptake. Uptake is expressed in total number of hours (h) and % uptake time is the total number of hours of potential uptake divided by the number of hours in the month. Figures for 85% RH and 90% RH are included to illustrate the differences caused by revising the model.

Month	80% RH Uptake		85% RH Uptake		90% RH Uptake	
	h	%	h	%	h	%
August	45	*17.9	24	*9.5	0	*0.0
September	6	0.8	3	0.4	0	0.0
October	9	1.2	3	0.4	0	0.0
November	267	37.1	240	33.3	171	23.8
December	27	3.6	9	1.2	3	0.4
January	0	0.0	0	0.0	0	0.0
TOTAL	*351*	*10.8*	*279*	*8.5*	*174*	*5.3*

* The % figures for August are based only on the number of hours for which records are available, i.e. from 21 August onwards, and therefore are not for the entire month.

Exposed lichens therefore are unlikely to absorb water from this air. The microclimate humidity increases during snow falls and at times of summer melt and at these times exposed lichens are able to absorb sufficient water to photosynthesise.

The timing of the changes in atmospheric RH, coupled with the very long days of the Antarctic summer, were such that most of the water uptake occurred during daylight hours. Of the total 351 hours during which water vapour uptake was sufficient for photosynthesis to occur, 300 hours was during daylight, as evidenced by a positive net radiation balance, and for 237 hours the PPFD was above 50 μmol m^{-2} s^{-1}, the minimum light level for positive net assimilation at most thallus temperatures for *Usnea sphacelata* (Kappen 1983). Therefore, it is likely that photosynthesis could occur for at least 67% of the time in which water vapour uptake was possible. This is not surprising, since diurnal patterns in microclimate would influence the amount of free water available and hence the local atmospheric humidity, with highest levels occurring during the warmer daylight hours.

The onset of the summer melt is obvious from Figure 6.1 where a marked change in Ψ_{air} can be seen to occur in mid-October. Although

it is unlikely that exposed lichens could absorb water vapour from the atmosphere during the second half of October and the first half of November, it is possible that lichens covered with snow were metabolically active during this phase. From approximately 10 November even completely exposed lichens were likely to be photosynthetically active due to water vapour uptake alone. The first instance of photosynthetic activity after the winter was observed on 5 October, a day with high humidity, high light and relatively high thallus temperatures, on which *Umbilicaria decussata* thalli were observed to be hydrated and evolving oxygen during the early hours of the afternoon. A spike can be observed on Figure 6.1 at this date, hence field observations support the model.

The osmotic potential of a non-ideal solution such as cell-sap can be estimated from its freezing point (Salisbury and Ross, 1985). Melick and Seppelt (1994a) gave freezing points for *Umbilicaria decussata* from Clark Peninsula of approximately -16°C which corresponds to an osmotic potential of -19.5 MPa. Since our values of Ψ_{WU} are more negative than this, consideration should be given to the assumption that 80% is the minimum relative humidity for a dry continental antarctic lichen to absorb water. If we were to substitute RH = 85% into Eqn. 6.1 we would receive Ψ_{WU} values from -22.6 MPa to -17.3 MPa which are very similar to the osmotic potential calculated from freezing point, and the substitution of RH = 90% gives a range of -14.6 MPa to -11.2 MPa. These figures of the osmotic potential indicate that RH = 85% is the most realistic figure for the atmospheric humidity at which water vapour uptake is sufficient to initiate photosynthesis. Such an elevation of the minimum RH value for water uptake reduces the potential for photosynthesis from absorption of water vapour even further (Table 6.1).

Earlier field work showed that exposed lichens in continental Antarctica are metabolically inactive for most of the summer period (Ch 7). This study indicates that the early part of the summer melt is probably the most important period for lichen photosynthesis and growth.

Chapter 7

Substratum nutrient levels and the distribution of lichen species

7.1 Introduction

The broadscale distribution of vegetation types in the Windmill Islands has been shown to be related to substratum type, the activity of penguins, aspect and proximity to the coast (see Ch. 2). Earlier studies also correlated vegetation patterns in the area with substratum nutrient levels and water availability (Hancock and Seppelt 1988, Smith 1990). Smith (1990) investigated the distribution and abundance of the principal bryophyte and lichen species in detailed transects along environmental gradients. On both Clark and Bailey Peninsulas, the presence of abandoned penguin rookeries was found to have a marked effect on the distribution and abundance of species (Ch. 2, Smith 1990, Melick *et al.* 1994).

This study examines, in detail, the effects of nutrient status and exposure on the distribution and abundance of lichen-dominated vegetation in a well vegetated site on Clark Peninsula. The aim was to determine what effects differing levels of substratum nutrients have on the patterns in the vegetation mosaic of species-rich lichen-dominated sites. There are a number of abandoned penguin rookeries on both Clark and Bailey Peninsulas (Goodwin 1993, Melick *et al.* 1994; Figure 7.1). Sites such as these offer a large range of substratum nutrient levels in a small geographic area and, as such, are suitable for the investigation of nutrient effects on vegetation patterns. For this study, an abandoned penguin rookery topping a small rounded knoll on Clark Peninsula was selected. The topography of this knoll, along with meso- and microclimatic conditions, are described in Ch. 3.

Figure 7.1 An abandoned penguin rookery on Bailey Peninsula with several erratic boulders. Note the extensive pebble field on the crest of the hill.

7.2 Materials and Methods.

The knoll was mapped at a scale of 1:500 with a 0.5m contour interval from stereo pairs of aerial photographs taken in mid-summer 1993-94 (see Ch. 3). This map was used to generate a profile along a transect running approximately north over the crest of the hill for 128m to the edge of a valley. North of this point, terrestrial vegetation ceased, since the valley is semipermanently filled with ice and snow. Vegetation was recorded in 25x25 cm quadrats placed each metre along the transect for the first 40m and thence every second metre. A pilot study indicated that these spacings and this quadrat size were optimal for sampling the diversity and cover of lichen species at this site. Total vegetation cover was estimated, as well as cover of each species present, using a modified Braun-Blanquet cover scale (see Figure 7.2). Specimens whose identity was difficult to ascertain in the field were collected and returned to the laboratory for identification.

Vegetation data were subjected to ordination and classification with a desktop computer using two-way indicator species analysis (TWINSPAN, Hill 1979). TWINSPAN is known to produce good separation of sociations where environmental determinants are strong (Belbin and McDonald 1993), and so is considered suitable for the investigation of pattern in vegetation of continental Antarctica.

A sample of the surface substratum was collected for nutrient analyses every 5 m along the transect over the crest of the knoll and every 10 m down the north facing slope. Soil pH was determined on fresh soil samples in 0.002 M $CaCl_2$ (Aitken and Moody 1991). Soil samples were dried at 60°C for two days and then subsamples taken for the various nutrient analyses. Soil organic matter was estimated by loss upon ignition in a muffle furnace. Total soil nitrogen was determined using the Kjeldahl method adapted from Emteryd (1989). Approximately one gram of finely divided soil was digested in 10mL of concentrated H_2SO_4 for 40 - 60 minutes on a digestion block at 400°C. Digests were cooled, diluted with 40 mL of deionised water and placed into a Tecator steam distillation unit where approximately 40 mL of 35% NaOH was added. Steam was bubbled through the digest for no less than four minutes and the distillate collected in a flask containing 25 mL of 4% HBO_3 with bromcresol green/methyl red indicator. The collected distillate was back titrated to end-point using 0.1N HCl. Total extractable phosphorus was estimated for samples digested in

concentrated nitric acid in a Milestone microwave digestion system. Samples were diluted with deionised water to 50 mL and analysed using the molybdate colourimetric method with $SnCl_2$ in HCl as a reducing agent. Optical density at 700 nm was determined after 30 min. Total extractable Na, K, Mg, Ca were estimated on diluted acid digested samples in a Varian Spectraa 400 atomic absorption spectrometer with matched standards and consideration for matric effects.

7.3 Results

7.3.1 The physical and chemical environment

Figure 3.1 is a topographic map of the study site showing the transect line as well as the site of the abandoned penguin rookery and the ice-rock interface. Figure 7.2 shows a profile diagram of the knoll along the transect line. The substratum structure is dominated by metamorphic schists and gneisses with smaller amounts of migmatite, charnockite and granite. Small to large erratics occur throughout the area, particularly near the crest of the knoll. A large, uninterrupted pebble field occurs from about 9 m to 23 m along the transect, evidence of a long abandoned rookery for Adélie penguins (*Pygoscelis adeliae*). This area consists of small, rounded pebbles from 5 to 15 cm in diameter, and occasional bleached penguin bones, feathers and egg shells. The region from 23 to 30 m along the transect comprises a smaller pebble field occurring amongst small gneissic outcrops and several granitic erratics of about 1 - 2 m diameter. The soils in these sites are fine and silty, mostly derived from penguin guano, as evidenced by the relatively high percentage of organic matter. The remainder of the transect is dominated by metamorphic bedrock covered by skeletal gravel soils.

Substratum chemistry is presented in Table 7.1. Soil pH was uniform across the hill (mean pH 4.29) with only one site near the crest being less acidic (pH 5.45), reflecting the past activity of penguins. The crest region is very much higher in extractable K, Mg, Na, Ca and total P and significantly higher in organic material, than either of the slopes. Differences in total soil nitrogen were much smaller than for other nutrients, but the crest region still showed higher levels than the slopes.

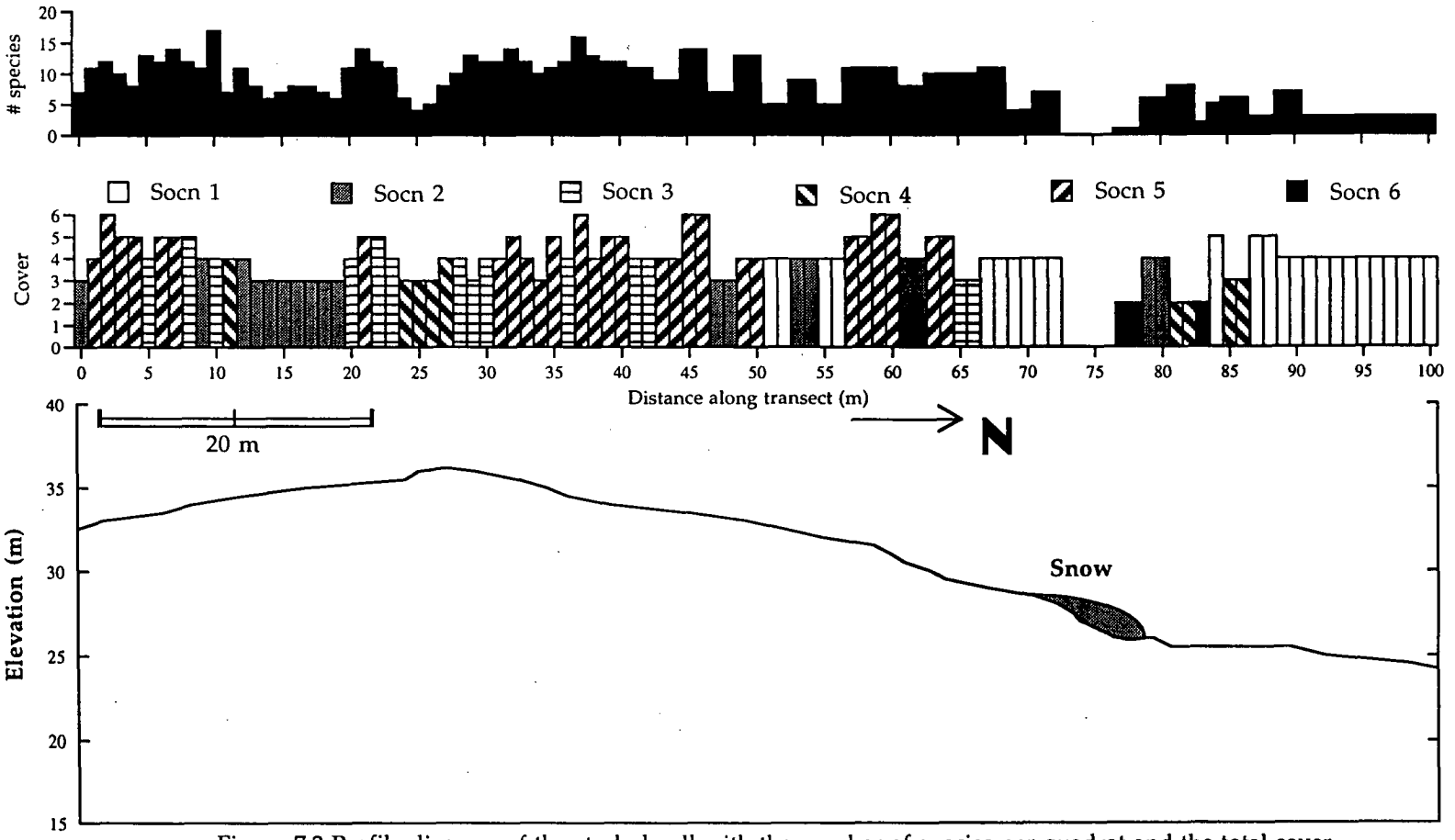

Figure 7.2 Profile diagram of the study knoll with the number of species per quadrat and the total cover and type of vegetation. Sociation (Socn) numbers refer to those defined in Table 7.3. Cover scale is 1=<1%, 2=1-5%, 3=5-25%, 4=25-50%, 5=50-75%, 6=75-100%.

TABLE 7.1. *Penguin knoll substratum chemistry. Site distance along transect is given in metres. All values are means ±SE. Total P, exchangeable Ca, pH and organic matter were only determined for samples from seven sites.*

Site (m)	K ($\mu g.g^{-1}$)	Mg ($\mu g.g^{-1}$)	Na ($\mu g.g^{-1}$)	N ($mg.g^{-1}$)	P ($mg.g^{-1}$)	Ca ($mg.g^{-1}$)	pH	Organics (%)
0	72 ±2.8	34 ±2.3	38 ±0.6	2.7 ±0.6	4.5 ±0.2	30.3 ±0.1	4.25 ±0.07	3.26 ±0.38
5	126 ±6.7	98 ±7.1	236 ±15.9	1.9 ±0.1				
10	90 ±1.3	56 ±0.5	104 ±2.2	1.4 ±0.3				
15	77 ±1.7	85 ±3.3	90 ±1.4	3.1 ±1.1	40.2 ±2.0	95.2 ±9.5	5.45 ±0.01	5.45 ±0.47
20	223 ±10.0	168 ±5.9	498 ±19.4	6.7 ±0.7				
25	107 ±2.7	67 ±1.3	128 ±3.9	5.1 ±0.1	21.8 ±3.4	41.5 ±8.1	4.17 ±0.03	13.87 ±1.01
30	178 ±2.4	14 ±0.7	37 ±1.9	0.8 ±0.4				
40	37 ±1.1	19 ±1.1	46 ±6.0	1.7 ±0.3	2.7 ±0.5	1.7 ±0.2	4.41 ±0.05	3.42 ±0.14
50	76 ±3.8	29 ±3.3	61 ±6.0	1.9 ±0.1				
60	82 ±3.5	14 ±1.0	46 ±4.9	1.3 ±0.0	1.3 ±0.5	1.0 ±0.1	4.27 ±0.01	2.72 ±0.36
70	71 ±1.2	29 ±1.7	27 ±2.8	0.6 ±0.1				
80	22 ±1.9	8 ±0.2	23 ±2.2	0.7 ±0.1	1.2 ±0.2	0.5 ±0.1	4.29 ±0.04	4.93 ±0.43
90	33 ±1.6	16 ±1.4	38 ±1.5	3.6 ±0.1				
100	29 ±1.2	11 ±0.3	17 ±0.2	2.8 ±0.9	1.0 ±0.2	0.7 ±0.0	4.36 ±0.02	6.07 ±1.24

7.3.2 Vegetation patterns

At least 25 species of lichen occur at the study site along with the moss *Grimmia antarctici* and large patches of moribund moss. Table 7.2 shows the frequency occurrence for each species along the transect. Detailed results of the species distribution and TWINSPAN analysis are given in Appendix A. The most common species were *Umbilicaria decussata, Pseudephebe minuscula, Usnea antarctica* and *Usnea sphacelata* (Table 7.2). Total vegetation cover along the transect and the number of species per quadrat is shown in Figure 7.2. Total vegetation cover ranged from <1% to 100%. The highest cover for any single species was 75% which was obtained by *Pseudephebe minuscula* and *Usnea sphacelata*. Figure 7.3 shows the cover of the major species across the knoll and Figure 7.4 shows the distribution of muscicolous species. Approximately 4% of quadrats along the transect were devoid of vegetation. All other quadrats contained from 1 to 17 species of lichen and moss with both the mean and median number of species per quadrat being 8.0. Approximately 30% of quadrats had from one to five species, 35% from six to ten and 35% contained more than ten species. The region with the lowest number of species occurred near the base of the north facing slope where late-lying snow occurs (Figure 7.2, Figure 7.5). Greatest species diversity was found either side of the hill crest in sites with varied microtopography and reasonably high nutrient levels (Figure 7.2). Species richness was also increased when moribund moss was present as this provided a habitat for several muscicolous species, most notably *Buellia grimmiae, Buellia papillata, Candelariella flava , Rinodina olivaceobrunnea, Lecanora expectans* and *Lepraria* sp. With the exception of *Rinodina olivaceobrunnea* and *Candelariella flava,* each of these species occurred only sparsely, although the moribund moss sometimes covered up to half the area of a quadrat (Figure 7.4, Figure 7.6). Where healthy *Grimmia antarctici* occurred the only muscicolous lichen species which was also present was *Buellia grimmiae,* even where some moribund moss was also present.

TWINSPAN analysis of the species cover data identified six sociations. Three of these were dominated by *Umbilicaria decussata,* while one was dominated by *Pseudephebe minuscula,* one by *Usnea sphacelata* and the last was defined by a sparse occurrence of saxicolous *Lecidea* spp. The six sociations are outlined in Table 7.3 and their distribution and total cover are shown in Figure 7.2.

TABLE 7.2. *Species list and percentage occurrence for the transect across the site.*

Species	% occurrence
Biatorella cerebriformis	1
Buellia frigida	25
Buellia grimmiae	20
Buellia latemarginata	13
Buellia lignoides	11
Buellia papillata	28
Buellia soredians	50
Caloplaca athallina	1
Caloplaca citrina	8
Candellariella halettensis	36
Grimmia antarctici	5
Lecanora expectans	16
Lecidea cancriformis	65
Lecidea sp.	28
Lepraria sp.	8
Moribund moss	46
Physcia caesia	10
Pseudephebe minuscula	89
Rhizocarpon flavum	6
Rhizoplaca melanophthalma	63
Rinodina olivaceobrunnea	28
Umbilicaria aprina	1
Umbilicaria propagulifera	<1
Umbilicaria decussata	94
Usnea antarctica	73
Usnea sphacelata	66
Xanthoria candelaria	8

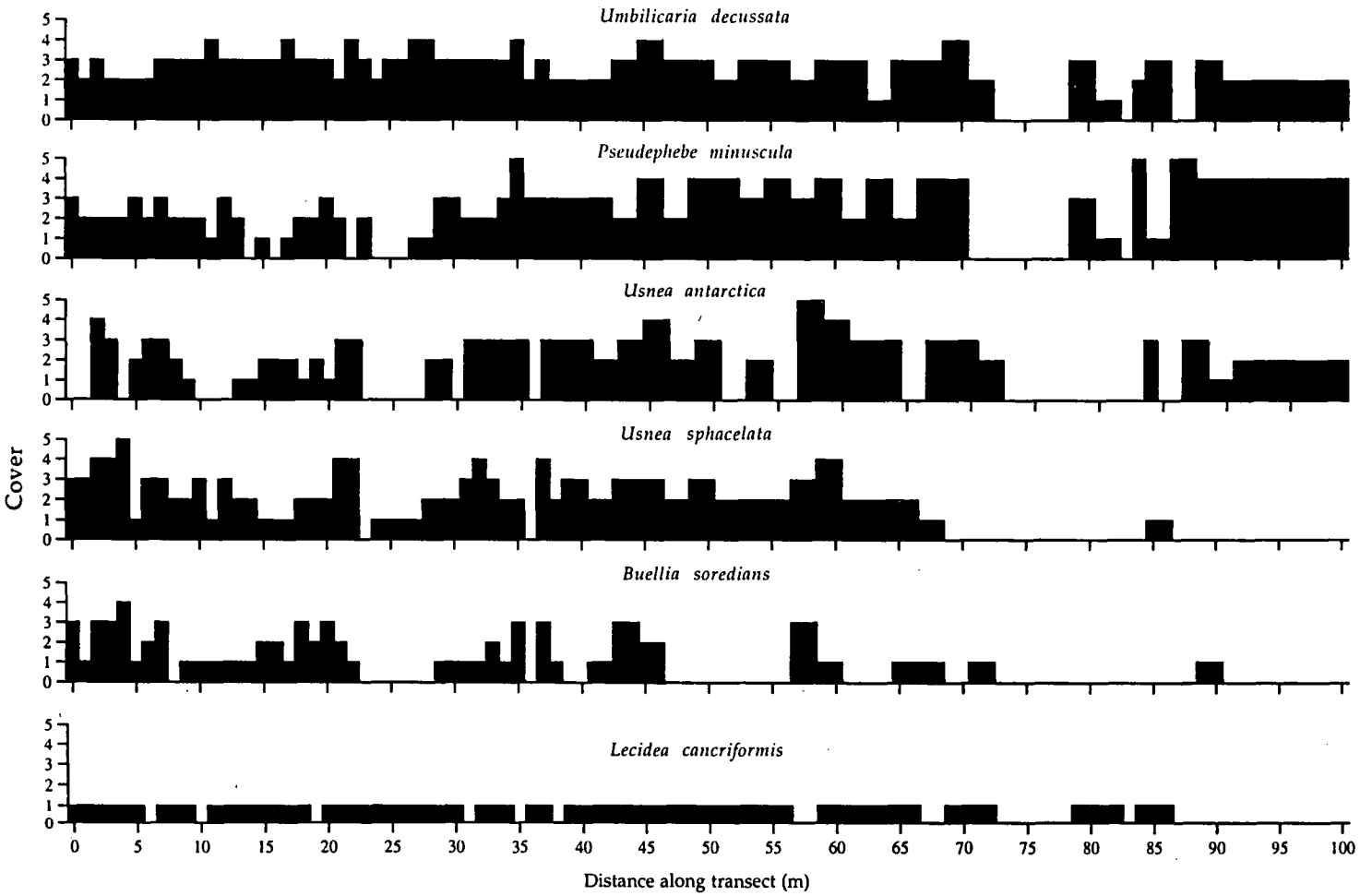

Figure 7.3 Distibution of the major species along the transect. Cover scale as for Fig. 7.2.

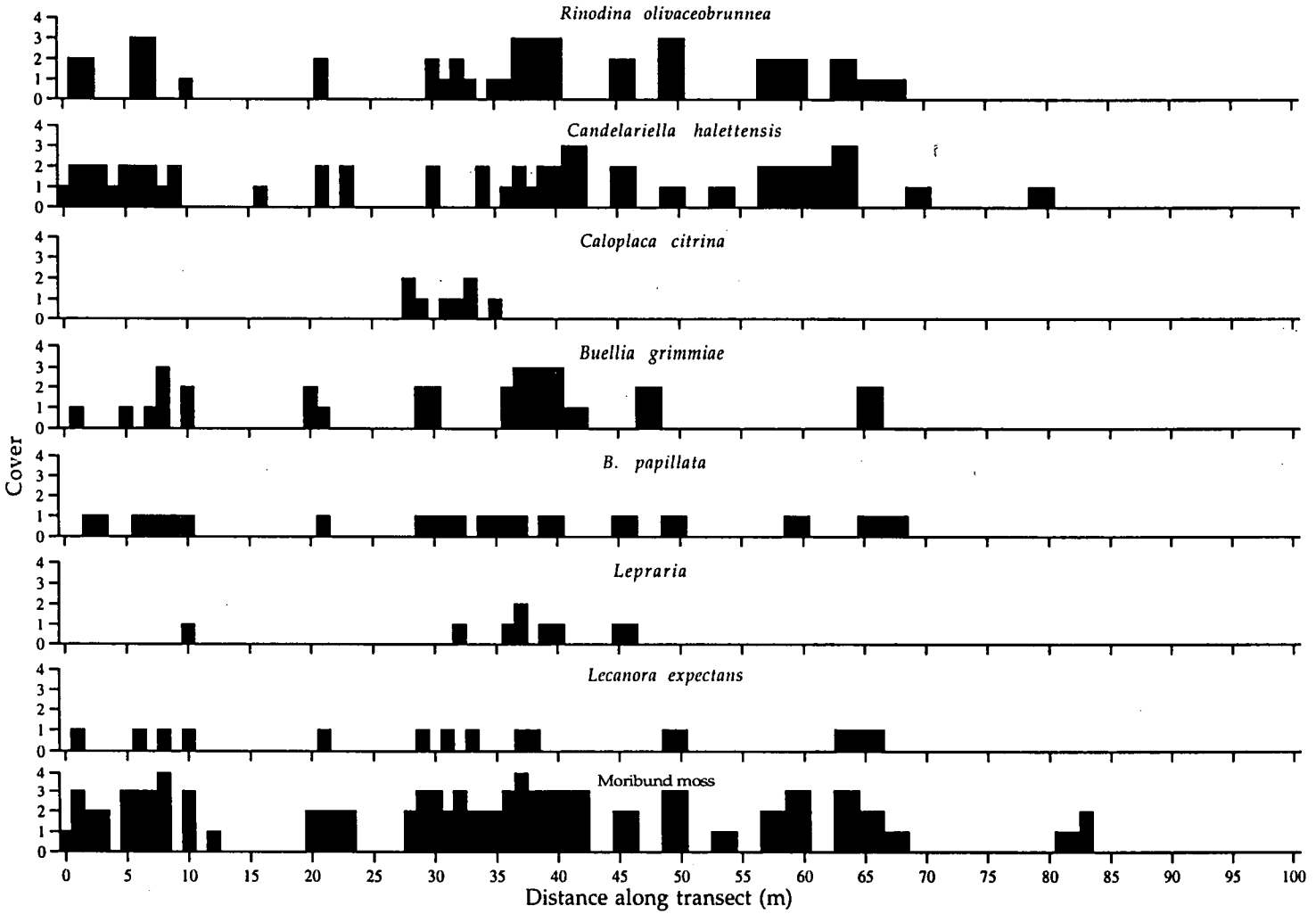

Figure 7.4 Distribution of muscicolous lichen species and moribund moss. Cover scale as for Fig. 7.2

Figure 7.5 The patch of semipermanent snow showing the areas bare of lichen growth at its edges.

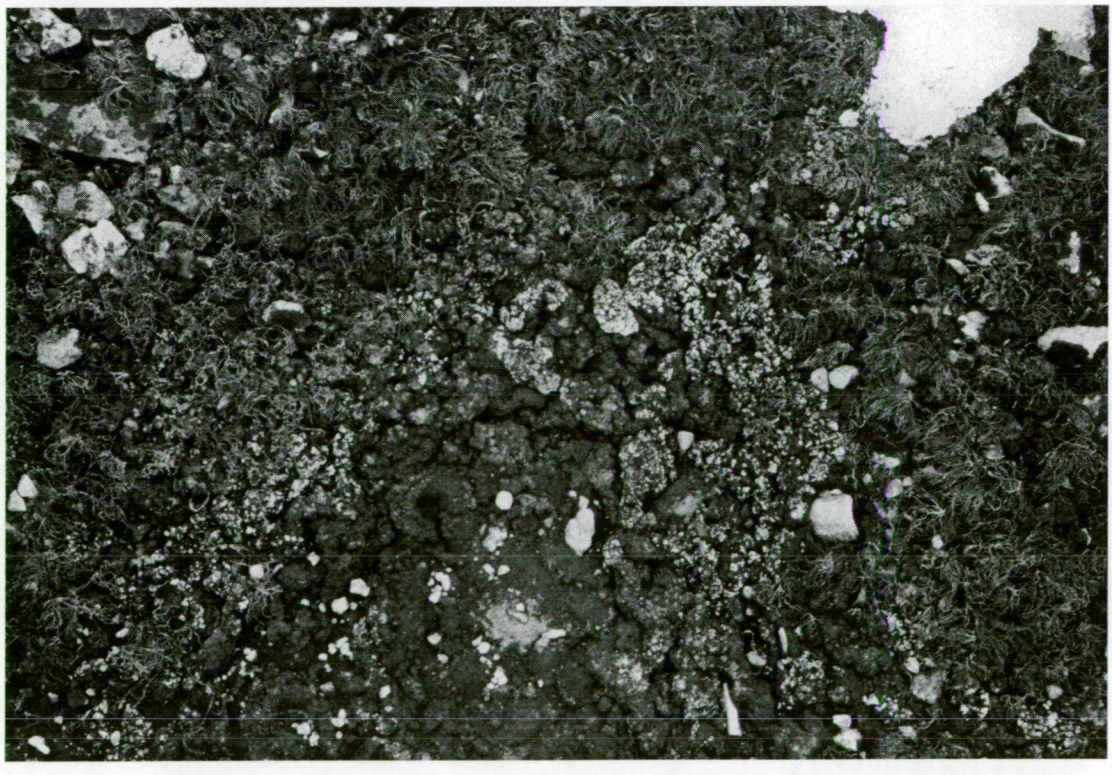

Figure 7.6 Moribund moss with muscicolous lichens including *Lepraria* sp., *Buellia grimmiae* and *Rinodina olivaceobrunnea.* Note also the abundance of *Usnea antarctica.*

TABLE 7.3 *Classification of vegetation communities at the study site on Clark Peninsula, Windmill Islands. The sociations were defined by TWINSPAN analysis and grouped subjectively.*

Antarctic non-vascular cryptogam formation

Fruticose, foliose and crustose lichen sub-formation

A. *Pseudephebe minuscula* dominated sociation.

Sociation 1. *Pseudephebe minuscula - Usnea antarctica - Umbilicaria decussata*

B. *Umbilicaria decussata* dominated sociations.

Sociation 2. *Umbilicaria decussata - Pseudephebe minuscula - Usnea sphacelata - Buellia soredians*

Sociation 3. *Umbilicaria decussata - Usnea sphacelata - Pseudephebe minuscula* - moribund moss - *Buellia grimmiae*

Sociation 4. *Umbilicaria decussata*

C. *Usnea sphacelata* dominated sociation.

Sociation 5. *Usnea sphacelata - Buellia soredians* - moribund moss - muscicolous lichen spp.

D. Other.

Sociation 6. Saxicolous *Lecidea* spp. (sparse)

The *Pseudephebe minuscula-Usnea antarctica-Umbilicaria decussata* sociation (sociation 1, Figure 7.7) occurred in approximately 28% of the quadrats, most of which were towards the base of the north facing slope, and as such was the dominant sociation at the site. The only interruption in the cover of this sociation in the lower northern slope was under the semi-permanent snow bank (Figure 7.5), where there was no vegetation, and at its edges where *Lecidea* sp. (sociation 6) and *Umbilicaria decussata* (sociation 4) occurred on small boulders. Sociations dominated by *Umbilicaria decussata* (sociations 2,3 and 4) occupy the crest of the knoll and the pebble field to the south of the knoll while the *Usnea sphacelata* sociation dominates nearly the entire upper half of the north facing slope. Vegetation dominated by *Umbilicaria decussata* alone (sociation 4, Figure 2.4a) occurred in the most exposed sites such as boulder tops and the pebble field to the

south of the crest. Where the microhabitat became slightly more sheltered and moister *Umbilicaria decussata* still dominated but *Usnea sphacelata, Pseudephebe minuscula* and moribund moss became more abundant (sociation 3). This also occurred where there was a gneissic outcrop which provided many sheltered microhabitats for *Pseudephebe minuscula* and *Usnea sphacelata* growth (Figure 7.8). Sociation 2, in which *Umbilicaria decussata* and *Pseudephebe minuscula* co-dominate with *Usnea sphacelata* and *Buellia soredians,* occupied almost all of the large pebble field. Although this habitat is very exposed, the polished surfaces of the pebbles are suitable for the sparse growth of closely appressed thalli of *Umbilicaria decussata* and *Pseudephebe minuscula,* with *Usnea sphacelata* , and less commonly *Usnea antarctica,* growing in the spaces between the pebbles. *Buellia soredians* was always found growing under a cover of *Usnea sphacelata* in this area. The centre of the pebble field was totally devoid of living or moribund moss.

Where the microtopography was variable, and therefore sheltered sites more common, *Usnea sphacelata* and *Buellia soredians* were dominant along with moribund moss and the associated muscicolous lichen species (sociation 5, Figure 7.9). The species richness of this sociation is high (11.8 species/quadrat) as compared to the overall species richness for the site (8.0 species/quadrat). Most of the muscicolous lichen species are most common in this sociation and several are restricted to it. All of the sites in which vegetation cover is greater than 75% are dominated by this sociation largely due to the abundance of *Usnea sphacelata.*

Usnea sphacelata is almost totally absent from the lower half of the north-facing slope as is moribund moss and the muscicolous lichen species. The region immediately above the semi-permanent snow patch is dominated by sociation 1 at a cover exceeding 25% up to the point where no vegetation exists. The lower side of the snow patch is characterised by a scant cover of *Lecidea cancriformis* and the very rare occurrence of other saxicolous *Lecidea* spp. and *Buellia* spp. *Umbilicaria decussata* and, to a lesser extent, *Pseudephebe minuscula* occur on the upper surfaces of small boulders for a few metres until sociation 1 again becomes dominant and remains so until the very edge of the ice-filled valley some 40 m further north. This lowest part of the north facing slope of the knoll is uniform in topography and

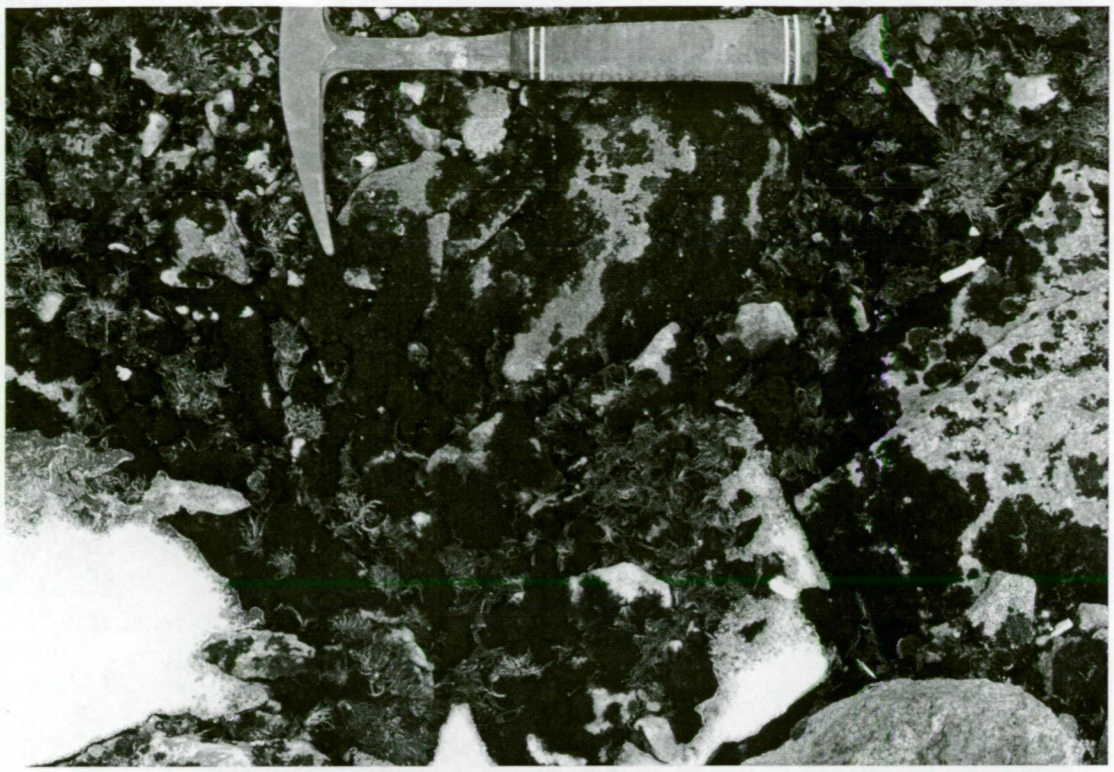

Figure 7.7 Sociation 1, showing the dominance of *Pseudephebe minuscula, Usnea antarctica* and *Umbilicaria decussata.*

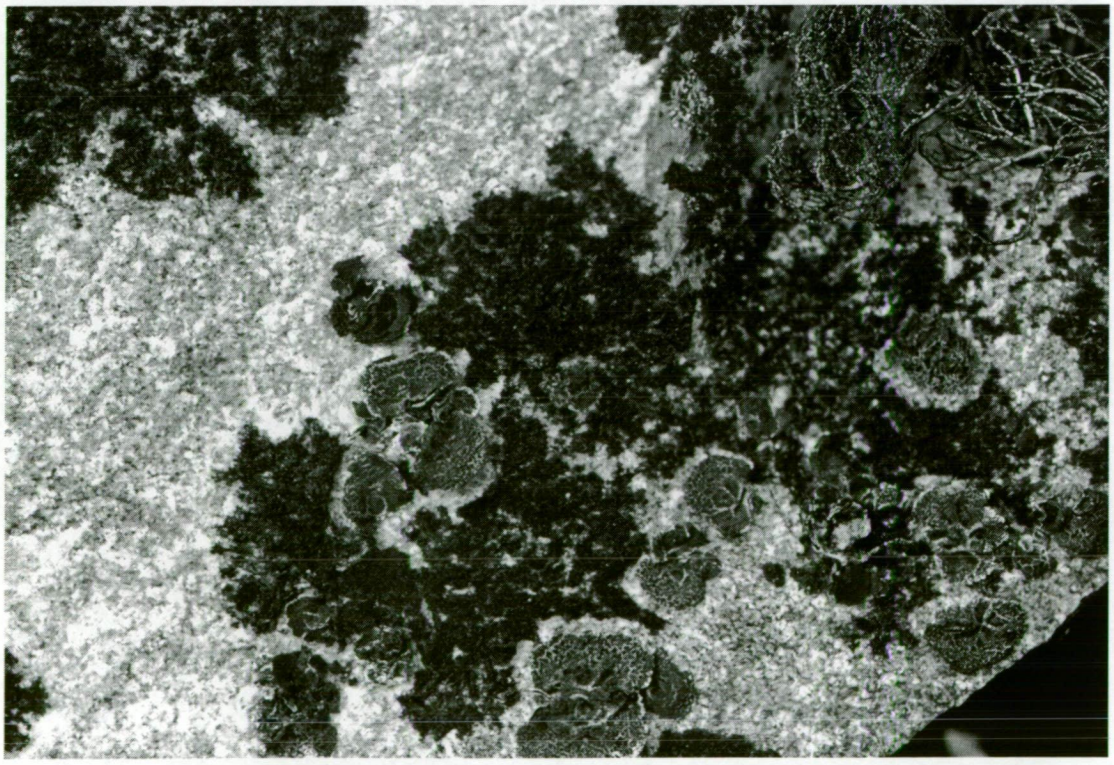

Figure 7.8 A gneissic erratic showing the three dominant species *Umbilicaria decussata, Pseudephebe minuscula* and *Usnea sphacelata.*

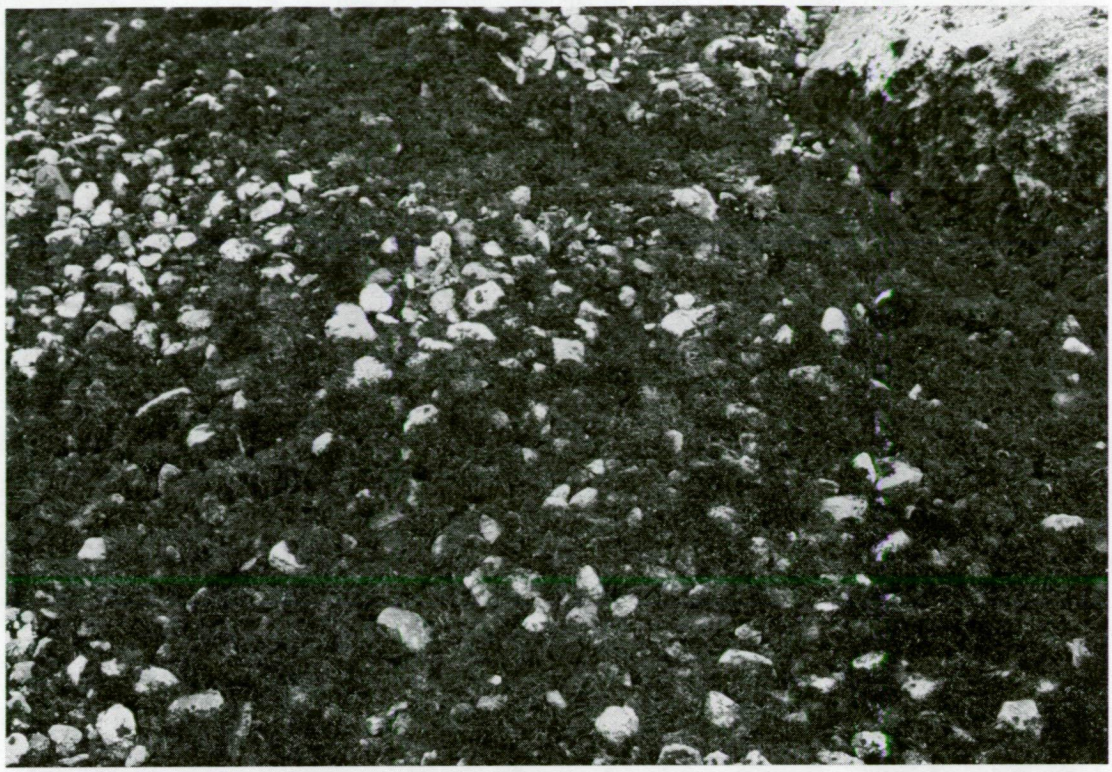

Figure 7.9 Sociation 5 in a nutrient-rich, sheltered site near the crest of the knoll.

Figure 7.10 *Lecidea cancriformis* displaying its endolithic nature.

completely dominated by *Pseudephebe minuscula*. In some flat gravelly areas *Usnea antarctica* forms a mat with *Pseudephebe minuscula* which totally covers the loose substratum. Both *Umbilicaria aprina* and *Umbilicaria propagulifera* are restricted to the lowest northern slopes of the knoll.

Lecidea cancriformis and *Rhizoplaca melanophthalma*, two of the most ubiquitous species at the site, occurred only in very low cover values because of their crustose to endolithic nature (Figure 7.10). These two lichens were present in all sociations but were less common in sociation 1, being absent from the most northern region of the knoll.

Many of the less common lichen species were totally restricted to the crest of the knoll. *Physcia caesia* occurred in the pebble field and on the lower edges of small boulders near the crest while *Xanthoria mawsonii* occurred only at the very summit of the knoll in the sociation dominated by *Umbilicaria decusssata*. *Xanthoria mawsonii* occurred in two definite forms here, one bright orange and one yellow-green, which always grew intermingled. *Caloplaca citrina* and *Caloplaca athallina* were also restricted to the crest of the knoll as was the very rare *Pleopsidium chlorophanum*. *Caloplaca citrina* and *Candelariella flava* at this site have a granular sorediose thallus and occupy much the same habitat on the surface of moribund moss. These two species never grew together, *Caloplaca citrina* occurring only in a small area at the crest. *Candelariella flava* occupied the niche everywhere else and could also be found growing directly on soil and rock surfaces, as well as on algae and lichens.

7.4 Discussion

The vegetation of the knoll on Clark Peninsula is well-developed and complex in comparison with other areas in continental Antarctica. Both the average vegetation cover of the site and the total number of species mark this as an exceptional site, even within the Windmill Islands. The varied microtopography of the knoll coupled with the large range of substratum nutrient levels provide suitable habitat for a large number of species within a small area. Such a site is ideal for the investigation of factors delimiting the distribution of lichen communities in Antarctica.

The major species at the site are the same as identified in most other studies of vegetation in continental Antarctica (Longton 1988). The classification of lichen communities presented here is similar to those identified by Smith (1988a) and further discussed by Melick *et al.* (1994). Sociations 1, 2 and 3 correspond to Smith's (1988a) Community Groups [2], [3] and [1a] respectively. This study also identifies two entirely new sociations (sociations 4 and 6) as well as one (sociation 5) which may be a variation of Smith's Community Group [7]. A further useful and interesting observation is that *Buellia soredians* is a major determinant of some lichen sociations in the Windmill Islands and it is likely that the presence or absence of this species from a lichen community including *Usnea sphacelata* yields information on microclimatic conditions.

Umbilicaria decussata is the dominant species at the site occurring in almost all habitats across the knoll in quite high cover (Table 7.2, Figure 7.3). None of the other species are as versatile in their habitat tolerance. The second most successful species is *Pseudephebe minuscula* which, although restricted by highly exposed conditions is otherwise ubiquitous. The two species of *Usnea* often co-occur and, although *Usnea sphacelata* is present in higher cover in exposed sites, *Usnea antarctica* extends into regions dominated by *Pseudephebe minuscula* from which *Usnea sphacelata* is absent. The dominance of *Pseudephebe minuscula* in regions of deeply-sheltered sites can be correlated with the photosynthetic parameters of this species which photosynthesises more rapidly at high thallus water contents than other species (see Ch. 5). Exposure has been shown to influence the codistribution of *Usnea* species in the Windmill Islands with *Usnea antarctica* being more abundant in sheltered and moister habitats (Hancock and Seppelt 1988). An interesting interaction is that between *Usnea sphacelata* and *Buellia soredians*. At all sites *Buellia soredians* occurs only under a cover of *Usnea sphacelata* and the cover of one species closely relates to the cover of the other.

Snowfall is common during the winter in the Windmill Islands, but the extremely strong winds regularly scour large areas free of snow. On most hill crests on Clark Peninsula snow gathers in the lee of rock outcrops and depressions in the substratum. Further down the slopes snow forms deep drifts due to the wind currents. Such drifts occur on the low slopes of the west, north and south faces of the study knoll. As

snow melts during the summer thaw, these places are the last to be exposed and therefore summer is correspondingly shorter than on the summit. The deep snow cover does, however, provide shelter from the harsh winter winds and a favourable microclimate in early summer (Kappen 1993). Exposure therefore can be ranked as a continuum ranging from exposed (boulder tops, the pebble field) through moderately sheltered (the upper slopes and the regions of exposed, uneven bedrock) to deeply sheltered (the lowest slopes).

One of the most striking aspects of the distribution patterns is the sharpness of the community boundary at the middle of the north-facing slope where the snow patch occurred. Further down the slope from this point most species are absent and sociation 1 dominates entirely. It is highly likely that this is due to the effect of late-lying snow. Late-lying snow is a major determinant of lichen distribution patterns elsewhere (Benedict 1990) and it is probable that only those species more tolerant of late-lying snow occur at the base of the slope. The region around the semi-permanent snow bank illustrates an extreme case where very few species exist at all and the area under the snow is totally devoid of vegetation.

There are definite patterns in the vegetation at the knoll. Most notable is the changing dominance of the major species from the crest to the base of the north face of the knoll. Various sociations involving *Umbilicaria decussata* (sociations 2-4) dominate the vegetation at exposed sites, particularly at the crest, on the abandoned penguin rookery and at the top of rock outcrops. Where the microtopography provides more shelter (moderately sheltered sites) the *Usnea sphacelata -Buellia soredians* sociation (sociation 5) is dominant. This sociation is the most dominant sociation at the site and represents the best developed community type anywhere in the Windmill Islands. Where snow drifts form during the winter (deeply sheltered sites) *Pseudephebe minuscula - Usnea antarctica - Umbilicaria decussata* (sociation 1) dominate and the vegetation becomes species poor although total cover values are high.

The lack of effect of substratum nutrients on the distribution of all the major species is interesting. The distribution of *Pseudephebe minuscula, Umbilicaria decussata, Usnea sphacelata* and *Usnea antarctica* can be explained by substratum structure and exposure.

Substratum nutrient levels are very important determinants of the distribution of many of the minor species, with several species occurring in nutrient-rich sites irrespective of other environmental variables. Such species-nutrient interactions have been identified before (Smith 1988a) and species occurring in nutrient rich sites have been termed nitrophilous (Smith 1988a, Longton 1988). Our results indicate that nitrogen may not be the major determinant of the distribution of these species since site differences in total nitrogen were slight compared to the enormous differences in other elements, particularly P and Ca. It is entirely possible, however, that present distribution patterns reflect past nutrient levels, since establishment may have occurred centuries ago before nitrogen compounds were leached and it is accepted that nitrogen is a major factor governing growth of lichens (Crittenden *et al.* 1994). Our measurements of total nitrogen also simplify a more complex scenario involving the distribution of nitrogen amongst various soluble and insoluble forms which differs over time (Speir and Cowling 1984).

Previous work from maritime Antarctica (Allen *et al.* 1967, Holdgate *et al.* 1967) proposed that most principal nutrients are not limiting to plant growth even in areas of the most severe leaching. It would appear from our results that major species are relatively insensitive to differences in substratum nutrient levels and growth is not inhibited by either abundance or lack of nutrients. The occurrence of lichen species along a nutrient gradient provides excellent conditions for the investigation of nutrient relations of these important components of the vegetation of Antarctica.

Chapter 8

Lichen nutrient content and its interaction with season

8.1 Introduction

This chapter investigates the relationship between substratum nutrient levels and the nutritional status of *Umbilicaria decussata* and *Usnea sphacelata* at the knoll described in Chapters 3 and 7. It also describes seasonal variations in the nutrient status of these two major lichen species.

Because of the effects of a significant local climatic aberration which occurred during the year, this chapter is divided into two major sections: the first section describes the event and its effects on the microclimate and lichens at the site, the second section describes the interaction of substratum nutrition with lichen nutrient status and its seasonal variability.

8.2 Effects of a rapid, unseasonal rewetting event on mineral location in lichens.

8.2.1 Introduction

This section aims to describe the effects on the vegetation of a rapid change in microclimatic conditions which occurred in the northern Windmill Islands region in the winter of 1992. General macro-, meso- and microclimatic conditions are described in Ch. 3.

Although it is well recognised that lichens from polar regions are highly resistant to frost injury, there have been few studies on the effects of freezing in the field. Most studies in which freezing tolerance is of interest look at the photosynthetic capability of lichens when frozen (e.g. Kappen 1989, Schroeter *et al.* 1994), or before and after rapid or deep-freezing (e.g. Kappen and Lange 1972), or after being frozen for extended periods (Larson 1978). While these experiments have great merit for the determination of photosynthetic and growth response to low temperatures, they are unable to determine the level of stress which is

occurring in the field, and the effects of any major disturbance, especially during the middle of the Antarctic winter, when photosynthesis is impossible.

A different method, which relies on the cation-exchange properties of lichens, is used here to investigate the effects of a highly unusual climatic event. This method is based on work of Buck and Brown (1979) who investigated the desiccation tolerance of lichens and mosses using a sequential elution technique.

A lichen acts as a cation-exchange complex, as evidenced by the high levels of pollutants and trace elements they can absorb (see Kershaw 1985). A diagrammatic representation of the cation-exchange nature of a lichen is presented in Figure 8.1. Lichens trap particulate matter in spaces between cells, and soluble material in this extracellular space can readily enter solution here. Insoluble matter in the particulate material may stay in the extracellular space and there is evidence that some particles remain unaltered for long periods (Nieboer *et al.* 1978), but, as Brown (1987) remarks, it is possible that over extended periods even relatively insoluble particles may dissolve. Mineral elements in the extracellular space can be eluted by washing with water.

The cell wall of lichens contains binding sites which can accumulate metal ions via a cation exchange process (Richardson 1995). This process involves fixed anionic sites which are likely to be carboxylic and hydrocarboxylic acids on or in the wall (Nieboer *et al.* 1976). Structural polysaccharides in the cell wall are the main sites of this interaction in some non-lichenised fungi (Muraleedharan and Venkovbachar 1994), but no studies have yet determined whether this is the case for lichens. The exchange process is preferential, with divalent cations displacing monovalent cations and heavier elements binding more effectively. This gives rise to a sequence of binding affinity; Cu, Pb>Zn>Ni>Mg>Sr (Brown 1987). Divalent ions displace each other stoichiometrically but they displace twice as many monovalent ions (Burton *et al.* 1981). This affinity can be used to elute and quantify ions from the binding sites on the wall simply by flooding the sites with an excess of ions of high affinity. Buck and Brown (1979) used a solution of Ni^{2+} to elute monovalent (e.g. Na^{+} and K^{+}) and divalent (Ca^{2+} and Mg^{2+}) mineral ions from the binding sites on lichen cell walls.

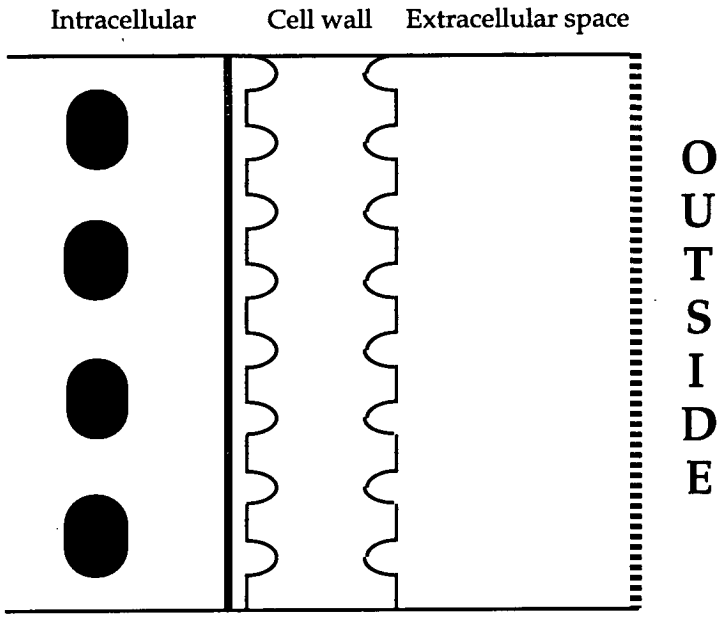

Figure 8.1 A diagrammatic portrayal of the various zones in the cation exchange nature of a lichen. The dotted line to the right indicates the partial boundary presented by the extracellular space. Binding sites are shown on the cell wall and the thick line represents the cell membrane. The solid shapes inside the intracellular space indicate structural fractions which are not exchangeable. See text for a detailed description.

The remainder of the mineral elements are located intracellularly. If the cell membrane is intact these elements can not be removed and analysed. Some investigations boil the tissue in water to burst the membrane and extract the cytoplasmic elements, so that any remaining elements are structural and can be freed by acid digestion of the tissues (see Brown and Wells 1988). Other investigations estimate only the total intracellular cation concentration by acid digestion of the tissues.

Since it is known that virtually all of the K is located within the soluble intracellular fraction (Brown 1987), the presence of large amounts of K in either the wall-bound or extracellular fractions indicates a loss of membrane integrity and the leakage of electrolytes. Magnesium is also useful in terms of assessing membrane integrity within a species, but the distribution of Mg within the thallus varies between species (Brown 1987), limiting comparisons.

The first section of this chapter describes the unusual climatic conditions which occurred during June 1992 and uses the cation exchange nature of lichens to assess the effects of these conditions on *Umbilicaria decussata* and *Usnea sphacelata*.

8.2.2 Materials and methods

Mineral element location was studied in *Umbilicaria decussata* and *Usnea sphacelata*. The samples were collected from a low rounded hill at the north-eastern end of Clark Peninsula approximately 4 km north of the current Casey station. The structure, vegetation, meso- and microclimatic conditions at this site have already been described.

Samples of both *Umbilicaria decussata* and *Usnea sphacelata* were collected from three sites: on the hill crest, and on the northern and southern aspects (Sites C1, NM1 and SF1 from Ch. 3). This was part of a larger monthly sampling regime (see Chapter 8.3). Samples were collected frozen and kept frozen until analysis. In early June the north face site was covered by approximately 30 cm of snow, the crest site was largely snow free, with a maximum snow depth of less than 5 cm, and the south face site was covered by at least one metre of firm snow. Microclimatic measurements were obtained from the data set described in Chapter 3. PPFD levels in the Windmill Islands are negligible throughout June.

All samples were prepared in triplicate and treated separately. Samples were washed in a beaker three times with 10 mL of deionised water followed by three washings with 10 mL of 20 mM $NiCl_2$ as per Brown (1987). The three washings were then combined and made up to 50 mL. A pilot study indicated that this method retrieved nearly all of the exchangeable cations with no significant increase in yield obtained by further washings. Lichens were then digested in concentrated nitric acid in a Milestone microwave digestion system according to the following protocol.

Approximately 100 mg of lichen thallus was weighed accurately into a container and digested in 5 mL concentrated HNO_3, using the power sequence given in Table 8.1. This sequence was determined after much experimenting and resulted in clear digests with no suspended matter and no measurable sample loss. The two steps of 0W prevented pressure from building to a level where sample loss would occur through chamber venting. After the digestion sequence the containers were left for approximately one hour to cool and then the digest was washed out of the container into a 50 mL volumetric flask with deionised, distilled water and made up to volume. All samples were analysed by a Varian

SpectrAA 400 atomic absorption spectrometer, with matched standards and consideration of matric effects. Three readings were taken for each sample.

Results were analysed by three factor ANOVA. Variances were checked for homogeneity by Cochran's test and those data sets which showed variance heterogeneity were transformed according to Sokal and Rohlf (1995).

TABLE 8.1 *Power sequence used in the microwave digestion of lichen samples.*

Step	Power (W)	Time (min.)
1	250	2
2	400	6
3	0	1
4	600	5
5	0	2
6	600	5

8.2.4 Results

The figures in Ch. 3, especially Figure 3.5 and Figure 3.6, indicate that the period from 15 to 19 June was atypical. During this period the ambient temperature rose sharply due to a severe blizzard and remained above freezing for approximately 60 hours before it returned to subzero levels (Figure 8.2). At approximately 2300h 18 June, 14 mm of rain fell in less than an hour. Shortly after this the temperature fell to subzero levels and the large amount of free water present froze resulting in a sheet of clear ice over most exposed surfaces.

The effect this had on thallus temperatures is shown in Figure 8.3. Thallus temperatures at the hill crest were closest to ambient throughout the rewetting event and slightly warmer than those from the north face. Lichens from the south face site were never exposed to temperatures above 0°C (Figure 8.3). The actual concentrations of elements in each location for both species at all sites are given in Appendix B.

Results of the analyses of variance are shown in Table 8.2. The data for intracellular K and extracellular Ca were heteroscedastic and could not be stabilised by any of the transforms recommended in Sokal and Rohlf

(1995). The location within the thallus of K, Na, Mg and Ca before and after the rewetting event at each of the three sites is shown in Figures 8.4 to 8.7. Figure 8.8 shows the results for non-intracellular K, which is the sum of extracellular and wall-bound K.

From Table 8.2 it is clear that the main effect of month is never significant and therefore the rewetting event had no overall effect on the location of any of the four mineral elements. The interaction of month with species (SxM) was significant for extracellular, non-intracellular and total K, while the interaction of species, level and month was significant for total Mg and K only. There was a significant interaction between level and month (LxM) only for wall-bound and intracellular Mg.

The main effects of species and level, however, were significant for the location of all elements. There was a significantly higher percentage of wall-bound K in *Usnea* than in *Umbilicaria*, and consequently a higher non-intracellular K (or lower intracellular K). *Umbilicaria* on the other hand had a higher percentage of its Na located extracellularly than did *Usnea*. Overall, *Umbilicaria* had a higher thallus concentration of Mg while *Usnea* had higher Ca levels. *Umbilicaria* had significantly more of its Mg located extracellularly and slightly more intracellularly than did *Usnea*, and this was at the expense of the wall-bound fraction. *Umbilicaria* also had a significantly higher proportion of its total Ca located extracellularly and wall-bound than *Usnea*, which means that *Usnea* had more of its Ca located intracellularly. The total concentration of Mg dropped between June and July in *Umbilicaria* from the north face and in *Usnea* from the crest, yet it increased markedly over the same period in *Umbilicaria* from the crest.

Extracellular K increased between June and July in *Usnea* from the crest region, but decreased in *Umbilicaria* from the same site. The total concentration of K in *Umbilicaria* from the crest region tripled between June and July yet there was little change in the percentage of non-intracellular K for this species at this site.

Differences between sites tended to remain more or less constant between the months, as indicated by the lack of a significant interaction between level and month (LxM) for all elements other than Mg (Table 8.2). The interaction of species, level and month (SxLxM) were only significant for total concentrations of K and Mg.

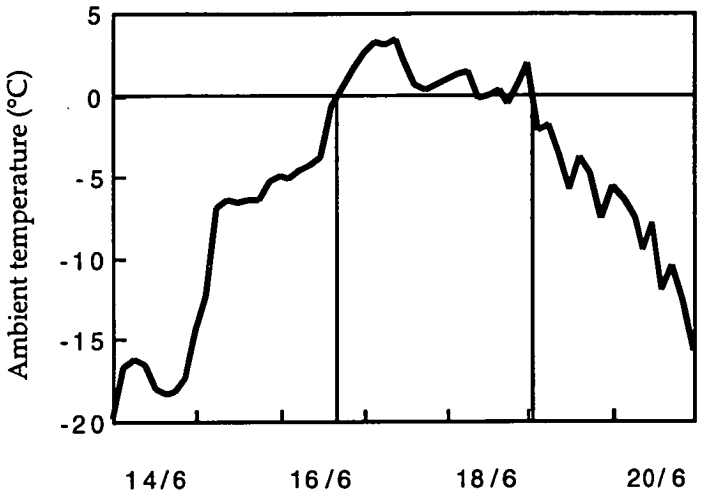

Figure 8.2 Ambient temperature before, during and after the unusual rewetting event in mid-June.

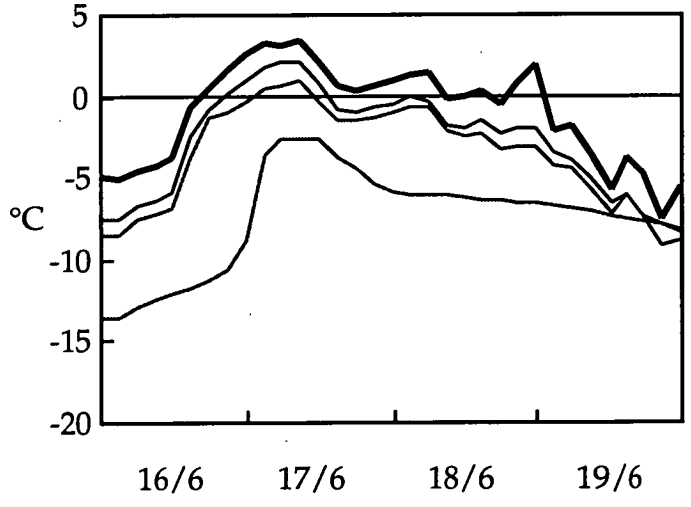

Figure 8.3 Ambient (black) and thallus temperatures at NM1 (red), C1 (blue) and SF1 (green) during the rewetting event in mid-June 1992.

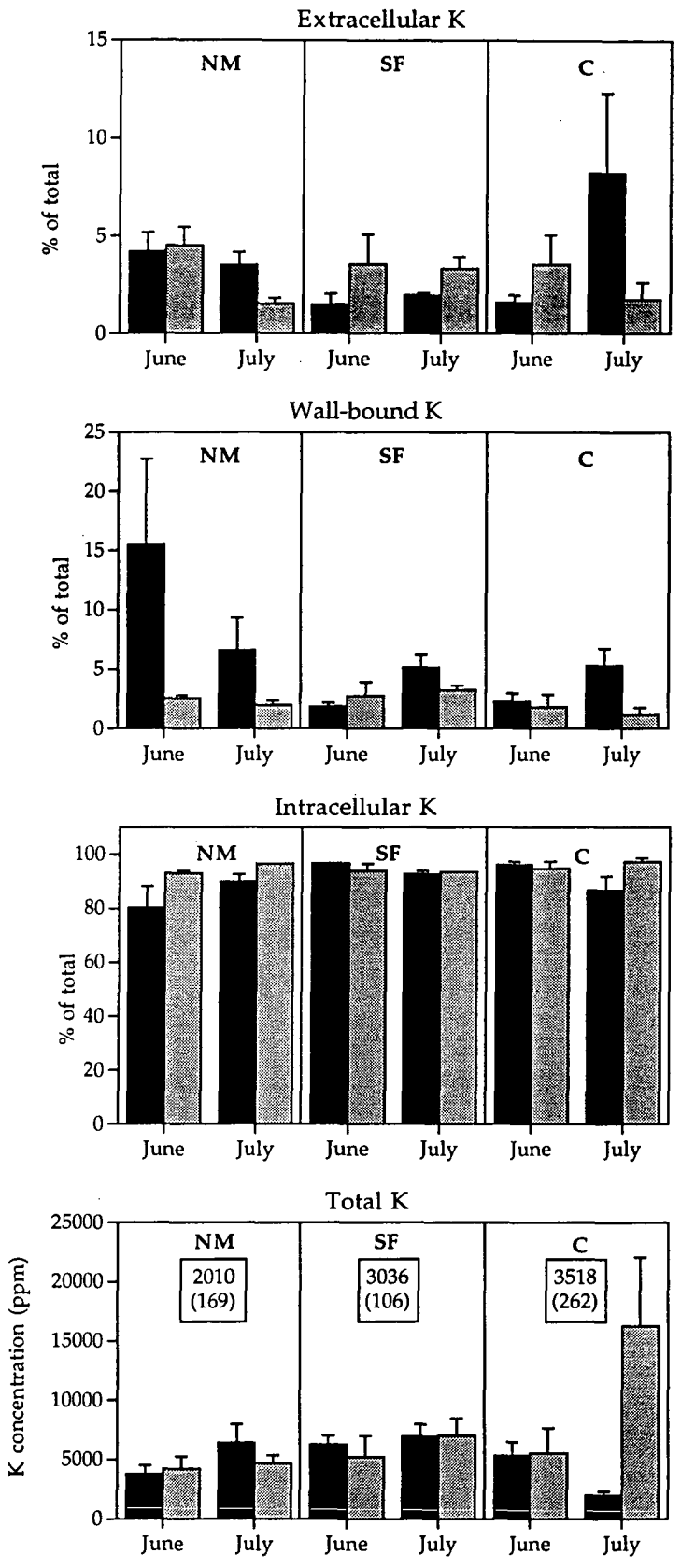

Figure 8.4 Potassium location in *Usnea* (solid bars) and *Umbilicaria* (stippled bars) from three sites before and after the rewetting event. Vertical lines are one standard error. Figures in boxes in the lowest graph are the substratum K concentrations in ppm with one standard error in parentheses.

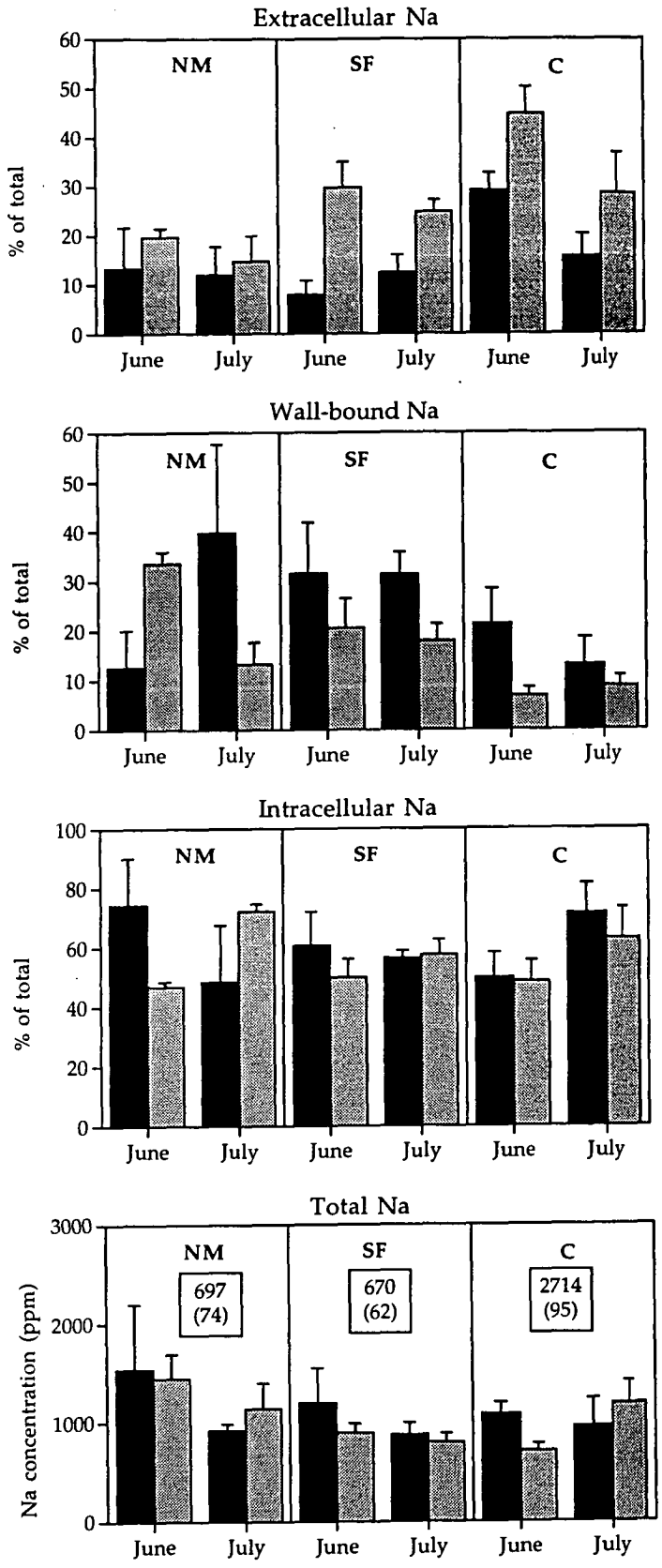

Figure 8.5 Sodium location in *Usnea* (solid bars) and *Umbilicaria* (stippled bars) from three sites before and after the rewetting event. Vertical lines are one standard error. Figures in boxes in the lowest graph are the substratum Na concentrations in ppm with one standard error in parentheses.

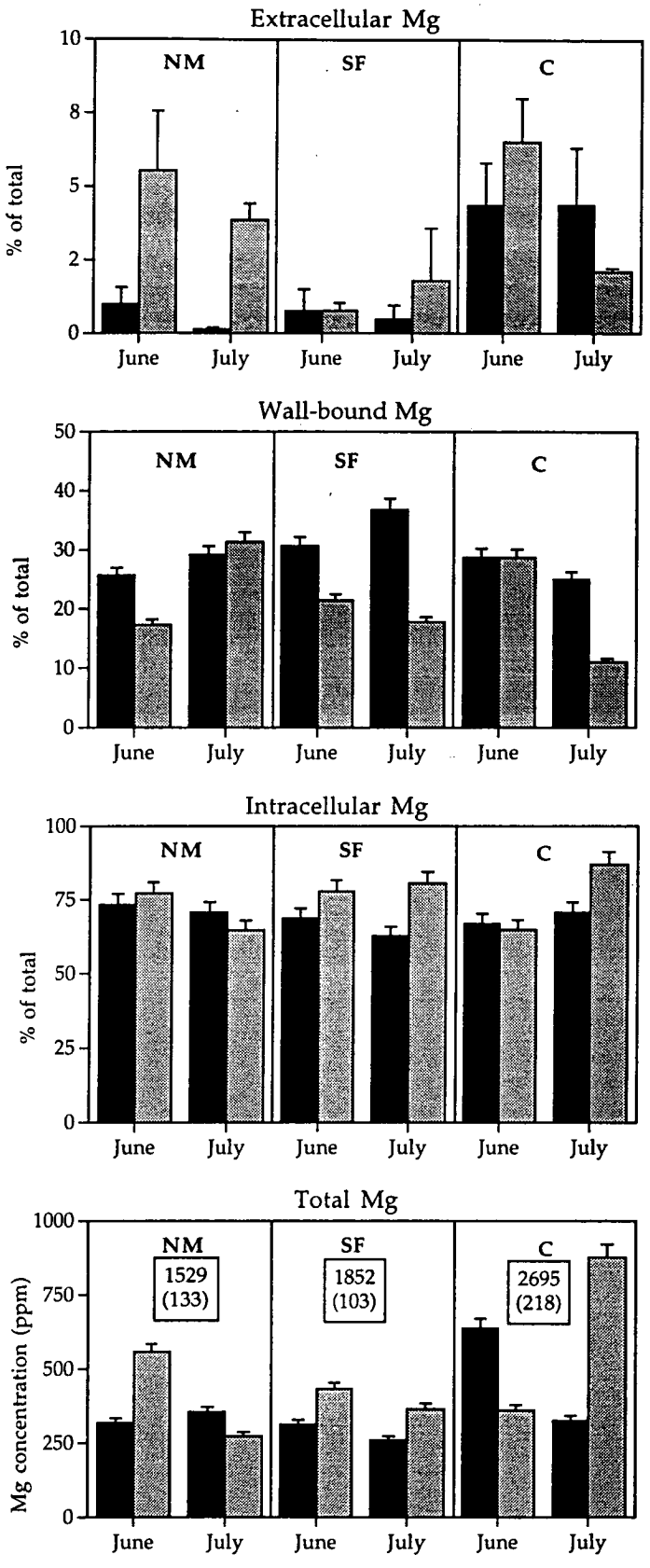

Figure 8.6 Magnesium location in *Usnea* (solid bars) and *Umbilicaria* (stippled bars) from three sites (NM, SF, C) before and after the rewetting event. Vertical lines are one standard error. Figures in boxes in the lowest graph are the substratum Mg concentrations in ppm with one standard error in parentheses.

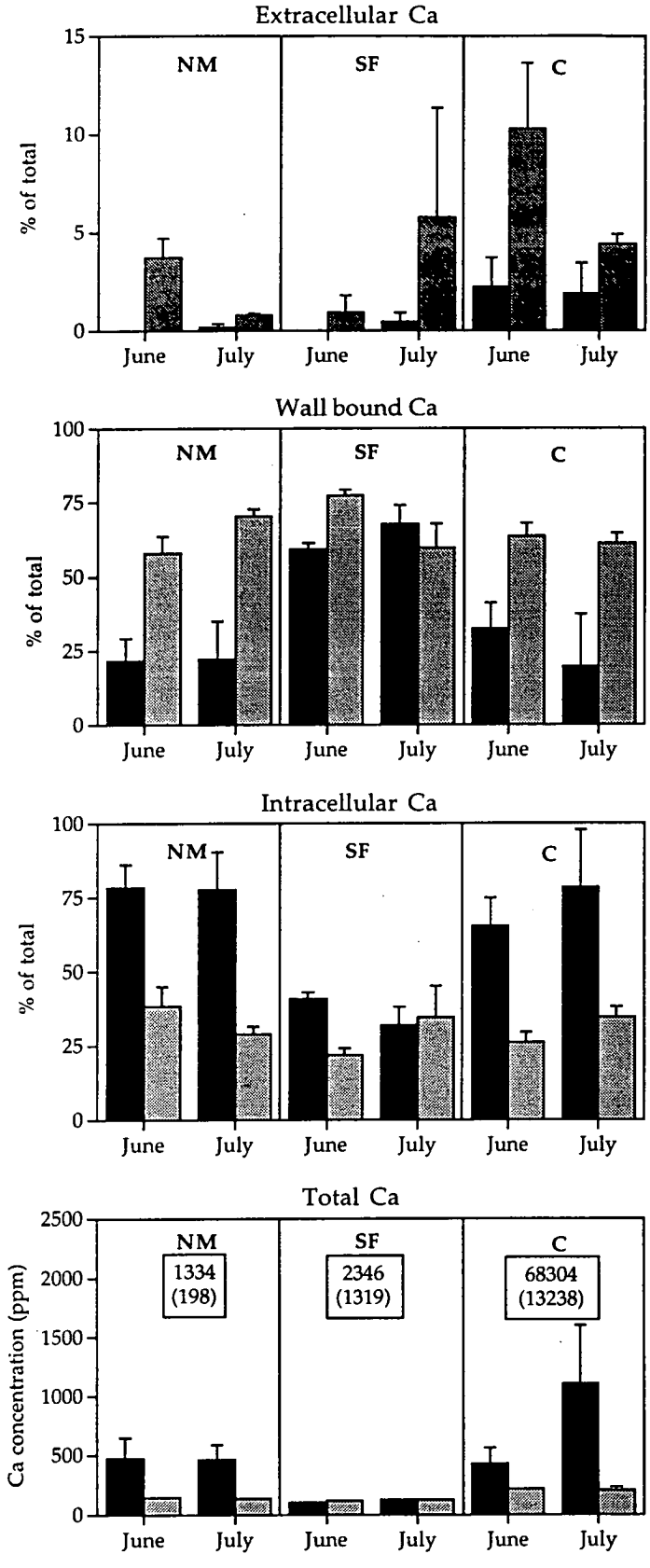

Figure 8.7 Calcium location in *Usnea* (solid bars) and *Umbilicaria* (stippled bars) from three sites before and after the rewetting event. Vertical lines are one standard error. Figures in boxes in the lowest graph are the substratum Ca concentrations in ppm with one standard error in parentheses.

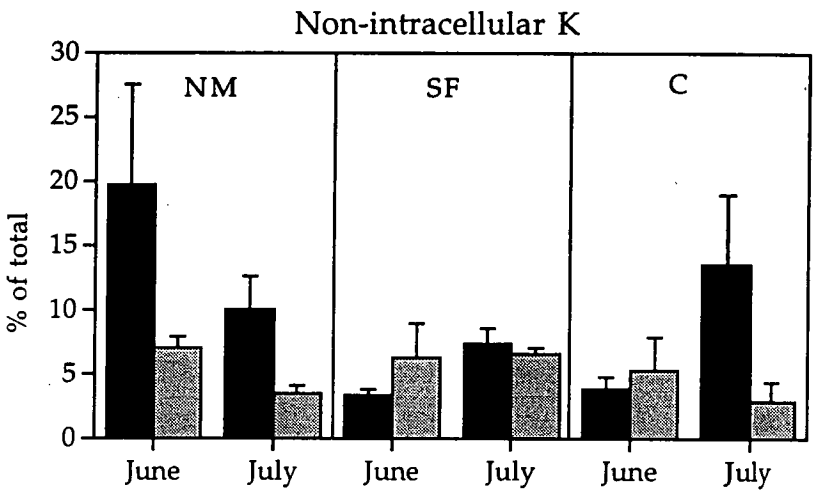

Figure 8.8 Non-intracellular K levels for *Usnea* (solid bars) and *Umbilicaria* (stippled bars) from three sites before and after the rewetting event. Vertical lines are one standard error.

TABLE 8.2 *F ratios from ANOVA of mineral location. * denotes value significant at p<0.05, ** denotes value significant at p<0.01.*

		Source						
Element & Location		Sp.	Level	Month	S x L	S x M	L x M	SxLxM
(degrees of freedom)		(1,24)	(2,24)	(1,24)	(2,24)	(1,24)	(2,24)	(2,24)
K	Extracellular	0.06	0.99	0.00	3.77*	10.01**	2.79	2.45
	Wall-bound	14.37**	4.53*	0.43	2.83	1.26	2.56	1.24
	Non-intracellular	6.58*	2.90	0.07	3.55*	5.21*	3.26	1.69
	Intracellular†	5.62	2.08	0.06	2.79	0.50	3.07	2.18
	TOTAL	1.62	1.04	1.75	4.27*	4.29*	0.14	4.97*
Na	Extracellular	16.23**	8.67	4.18	1.62	0.80	2.29	0.13
	Wall-bound	1.70	4.11*	0.06	1.77	1.11	0.04	3.39
	Intracellular	0.47	0.20	1.31	0.03	2.73	1.06	2.30
	TOTAL	0.01	1.22	0.57	0.36	1.02	0.74	0.59
Mg	Extracellular	5.94*	8.85**	2.64	3.45*	0.72	1.00	1.75
	Wall-bound	9.44**	0.68	0.00	1.68	0.87	4.34*	2.04
	Intracellular	4.93*	0.02	0.10	2.11	1.05	4.04*	1.86
	TOTAL	6.53*	9.06**	0.41	0.15	3.66	2.47	16.08**
Ca	Extracellular†	9.46	3.55	0.34	0.60	0.29	1.96	1.80
	Wall-bound	34.07**	11.07**	0.08	6.76**	0.08	0.79	2.12
	Intracellular	42.19**	10.37**	0.04	3.96*	1.38	1.07	2.16
	TOTAL	11.83**	10.74**	0.39	3.91*	0.60	0.20	0.24

† data were heteroscedastic and were not stabilised by transformation, therefore no inferences could be drawn from ANOVA and F ratios included merely for comparison.

8.1.4 Discussion

The very high ambient temperatures in the middle of the Antarctic winter were unusual in themselves, but when linked with the rain which followed, they presented an extremely rare episode. Winter temperatures near to 0°C are not unknown in the Windmill Islands, but they are a rare event and usually do not last for any length of time. The increase of ambient temperature from approximately -18°C to -6°C in just a few hours (Figure 8.2) is an example of the rapid warming which occurs immediately prior to the arrival of a blizzard, which is a common occurrence in winter in the Windmill Islands. The 60 hour period for which the temperature stayed above freezing during winter is unique in 38 years of meteorological records for the Windmill Islands (Pendlebury,

Australian Bureau of Meteorology, pers. comm.). Rain is almost completely unknown from the Windmill Islands, and heavy downpours in the middle of winter, especially so. Therefore the climatic conditions presented a unique opportunity to study the effect on lichens of a prolonged period of high thallus WC, warm temperatures and darkness followed by rapid refreezing when fully hydrated.

The differential accumulation of snow in the months preceding the rewetting event provided a perfect control for the natural field experiment, in that the south face site was insulated by such a thick layer of snow that thallus temperatures never reached 0°C and therefore it is unlikely that the thalli were exposed to liquid water. The thalli did, however, reach a temperature at which water uptake from the snow and metabolic activity were likely to be reasonably high (Schroeter *et al.* 1994). So the differences between the SF site and the others were limited to the exposure to temperatures above 0°C and to freezing when fully-hydrated, as it is likely that the lichens at the SF site gradually dehydrated as they froze. Those at the SF site were also protected from the very rapid drop to low temperatures over the few days to weeks following the rewetting episode (see Figure 3.5 and 3.6).

Surprisingly, the event did not affect the mineral location dramatically, and no main effect of month was found in either species, at any site (Table 8.2). There was however, some effect of month at some sites for some elements as evidenced by a significant interaction of month with species or level. These interactions have been described above. Most importantly, the location of K was significantly altered in *Usnea* from the crest site. Stressful conditions which lead to a loss of membrane integrity, such as might be expected to occur upon freezing a saturated lichen, should cause the leakage of K from the cytoplasm. In a lichen, it is likely that this K would be trapped by binding sites located in the cell-wall and extracellularly (Buck and Brown 1979). This has definitely occurred in *Usnea sphacelata* from the crest region (Figure 8.8) where the rewetting event was accompanied by an increase in both the extracellular and wall-bound fractions of K (Figure 8.4). *Usnea* from the north face, however, showed exactly the opposite, with a decrease in the non-intracellular fraction of K, although the significance of this change is marginal due to a large degree of variability between thalli. *Umbilicaria* showed little change in the location of K from June to July, regardless of site, with very little leakage of K occurring. Overall, the greater proportion of K which

occurred in the non-intracellular fraction in *Usnea* as compared to *Umbilicaria* indicates that *Usnea* is subject to a greater cellular stress than is *Umbilicaria*. It is not possible to link this higher stress to the rewetting event except at the crest region. The lower levels of K leakage at the SF site than at the other sites indicate that the insulating blanket of snow did protect *Usnea* from cellular stress.

The results, moreover, are different from those in which cellular stress was found to cause up to 50% of all K to leach from the cell (Buck and Brown 1979). Indeed, even the relatively high levels of non-intracellular K found in *Usnea* from the crest after the rewetting event are similar to those of the least stressed lichens in other studies. This is, perhaps, not that surprising given that lichens growing in continental Antarctica must tolerate numerous freeze-thaw events over the summer period and can survive freezing to extremely low temperatures (Kappen 1993).

The location of Mg is also thought to indicate stress, although this is dependent upon species. The amount of Mg located in the extracellular and wall-bound fractions is also more variable over time due to environmental inputs than is the case for K. The intracellular fraction of Mg varied only slightly between June and July which, once again, supports the relatively unstressed nature of the lichens. Interestingly, the large increase in the total Mg content of *Umbilicaria* from the crest translates directly into the intracellular fraction with a drop in the extracellular and wall-bound fractions. This indicates that *Umbilicaria* cells were absorbing Mg, either passively or actively, at the crest. The opposite occurred at the north face.

Changes in the extracellular fraction of all elements at the crest and north face sites can be partially attributed to the washing which the lichens must have experienced during the rewetting event. Since the concentration of the four elements in the melted snow and in the rain which fell at the end of the blizzard is unknown, it is not possible to say whether extracellular binding sites would have absorbed metal ions or lost them during this period. Wall-bound ions would not have been displaced by natural washing.

Differences between the species are interesting, particularly for Na, Mg and Ca. The greater proportion of extracellular Na in *Umbilicaria* than in *Usnea* may be due to the growth forms of the lichens, with the flattened,

foliose nature of *Umbilicaria* making its equilibrium closer to the substratum levels of ions. Since the overall Na concentration, as well as the wall-bound and intracellular fractions, are not different between the species, it seems likely that this is the case.

The high total Ca concentration of *Usnea* is related to its significantly higher proportion of intracellular Ca, which is completely constant between June and July (Figure 8.7). *Umbilicaria* maintained a relatively minor proportion of its Ca inside the cell, but kept somewhere between 50 and 75% of its total Ca bound to the wall, and very little in the extracellular space. *Usnea*, by comparison, had mostly low levels of Ca bound to the wall, but generally very high levels of Ca inside the cell and virtually none in the extracellular space. This trend is slightly different at the south face site, where more Ca is wall-bound and less intracellular, but there appears no obvious explanation for this. *Umbilicaria* obviously maintains a lower intracellular fraction of Ca than does *Usnea*, and must exclude Ca from the cell. The fraction of extracellular Ca rose in response to the substratum level of Ca, although the wall-bound fraction did not.

The total concentration of Mg was reasonably constant except in *Usnea* in June at the crest site, and *Umbilicaria* in June at the northern slope and July at the crest. There is no obvious reason for this pattern although the intracellular Mg fraction of *Umbilicaria* did rise significantly at the crest between June and July, while the extracellular and wall-bound fractions fell. This would seem to indicate an uptake of Mg. *Umbilicaria* also lost some intracellular Mg to binding sites on the wall between June and July. Although there is significantly more Mg in the intracellular fraction of *Umbilicaria* than in *Usnea*, the differences are much slighter than for Ca.

Overall, there are many differences in the mineral location details between the two species, with 10 comparisons out of a possible 15 being significant, six of these at $p<0.01$ (Table 8.2). Brown (1987) noted that differences between species are often due to different environmental inputs, even when growing at the same sites. Bosserman and Hagner (1981) found that in the same habitat some species' elemental composition may reflect wetfall and others dryfall and Brown (1987) showed that lichens growing intermingled on tree trunks may have vastly different distributions of mineral elements between species, even when the species are congeneric. These results will be discussed further

as part of the overall discussion of lichen nutrition and its interaction with time of year, site and species (section 8.3.4).

The technique used here to study membrane integrity is superior to conductivity measurements of electrolyte leakage (e.g. Belnap and Harper 1990), because information on the distribution of mineral elements within the thallus are obtained, and since membrane damage may not result in a large increase in water-exchangeable cations because of the binding sites on the cell wall.

8.3 LICHEN NUTRIENT CONTENT AND ITS INTERACTION WITH SUBSTRATUM NUTRITION AND SEASON.

8.3.1 Introduction

As pointed out by Kershaw (1985), the nutrient requirements of lichens have been very poorly studied in comparison to vascular plants. Very little is known about the nutritional requirements of lichens from any environment, despite its potential importance. It is not known, for example, if lichens absorb elements from their substratum, despite a growing body of cicumstantial evidence that this is the case. Most studies of the interactions of lichens with their mineral environment focus on heavy metals or other pollutants and the use of lichens as biological monitors of air quality. The majority of other studies concentrate on N_2-fixing cyanobacterial lichens and their importance as souces of available nitrogen in plant communities.

There have been a few studies which assess the effects of nutrition on the distribution and growth of lichens (e.g. Rogers 1990, Gremmen *et al.* 1995) but there is a general paucity of information on the nutritional relations of saxicolous lichens, particularly from Antarctica. This section aims to assess the effects on the nutrient status of *Umbilicaria decussata* and *Usnea sphacelata* of varying substratum nutrient levels, and to describe any seasonal patterns which occur. In order to do this, lichen samples were collected each month for a year from a number of sites across the knoll described in Chapters 3 and 7.

8.3.2 Materials and Methods

Nutrition of lichen thalli was studied at the eight sites indicated in Ch. 3. Two points were located at the base of the northern slope of the knoll (NB1 and NB2), two points were located approximately half way up the northern slope (NM1 and NM2), two in the crest region (C1 and C2) and two on the southern face just below the crest region (SF1 and SF2). The position of the each site is indicated on Figure 3.1 and is immediately adjacent to the points of microclimate measurement as described in Ch. 3.

Specimens of *Umbilicaria decussata* and *Usnea sphacelata* were collected at all sites at the beginning of each month from April 1992 until March 1993 by severing the lichen's point of attachment to the substratum with

a razor blade as close as possible to the rock surface. Lichens from each site were placed into plastic bags, taken to the laboratory and kept in a freezer at -18°C until analysed. Lichens were then removed, dried in paper bags in the dark at 20°C and divided for the various analyses. For the first month of collection (April 1992) lichen thalli were weighed when wet and again after being dried in order to determine thallus water content.

Samples were digested using a Milestone microwave digestion system and the protocol described in section 8.2.2 above. Phosphate determinations were made using the molybdate colourimetric method described in Ch. 7. Cation concentrations were determined by flame atomic absorption spectroscopy, as described in Ch. 7. Total thallus nitrogen was determined separately using approximately 100 - 200 mg of thallus. The lichen was added to a large test tube and digested in 10 mL of concentrated H_2SO_4 with a Tecator Kjehltab catalyst tablet for 40 - 60 minutes at 400°C in a Tecator digestion block. Total N was then estimated as described in Ch. 7.

All results were then expressed as a function of thallus dry weight, and analysed by analysis of variance. Data which demonstrated heteroscedastic variances were transformed according to Sokal and Rohlf (1995) and the transformed data analysed. Those means found to be significantly different at $p<0.05$ were compared using the Ryan-Einot-Gabriel-Welsch Multiple Range test (Sokal and Rohlf 1995).

8.3.3 Results

8.3.3.1 Substratum chemistry.

Substratum chemistry of the study knoll and its effect on lichen distribution is described in Ch. 7, but the specific details of the actual sites of lichen collection are described here so that their interaction with the nutritional status of major lichen species can be investigated. The substratum nutrient contents for the major elements are shown in Figures 8.9 and 8.10 and the remaining substratum nutrient details are given in Table 8.3. The sites vary enormously in terms of substratum elemental composition. The crest region is 100-fold higher in Ca than the NB sites and much higher in N, P, Zn, Cu, Mn and organic matter. The other sites are intermediate in these variables. There was no discernible trend in Mg, Fe and Al content, although the sites did differ. The NB

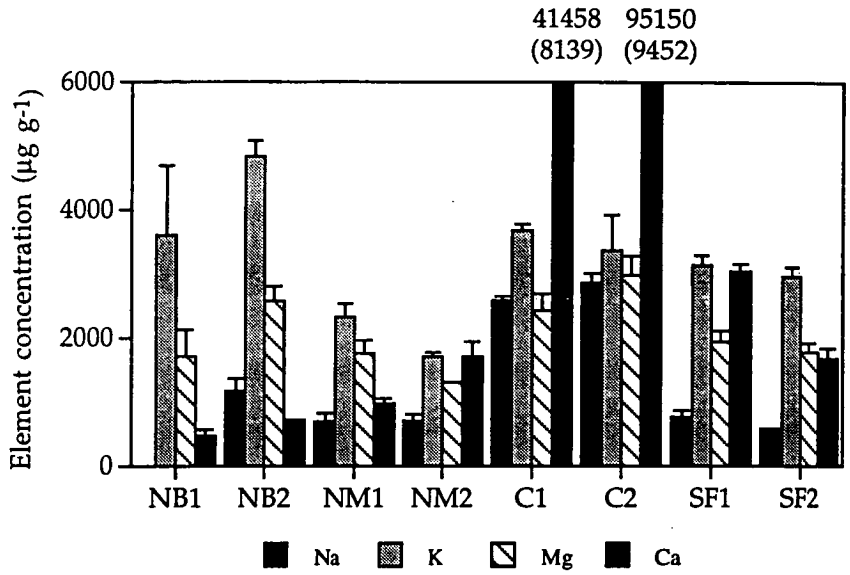

Figure 8.9 Total soil mineral element content. The number above the Ca bars at C1 and C2 are the means with standard errors in parentheses.

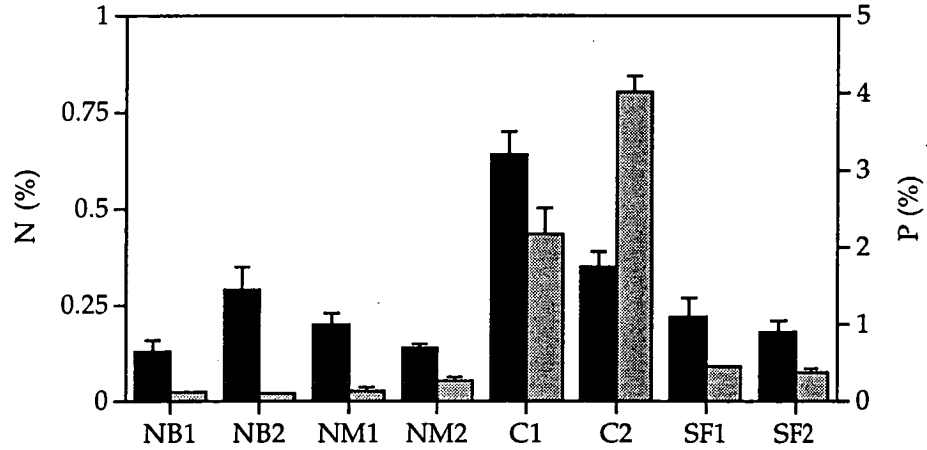

Figure 8.10 Total soil N (solid bars) and extractable P (stippled bars). Vertical lines are one standard error.

TABLE 8.3 *Details of substratum chemistry for each of the eight sites of lichen collection. Site names are the same as in Fig. 3.1. All values are means ± standard error.*

	Site							
Element	NB1	NB2	NM1	NM2	C1	C2	SF1	SF2
Fe ($\mu g\ g^{-1}$)	11409 ±1872	14616 ±3534	9796 ±810	6758 ±146	8748 ±2468	8888 ±88	10713 ±564	11074 ±326
Zn ($\mu g\ g^{-1}$)	16 ±3	23 ±3	14 ±1	19 ±1	224 ±28	452 ±73	30 ±1	25 ±2
Al ($\mu g\ g^{-1}$)	5946 ±938	8472 ±1034	3691 ±164	4051 ±179	6940 ±352	6649 ±830	5711 ±174	4821 ±420
Cu ($\mu g\ g^{-1}$)	9 ±1	41 ±19	11 ±1	18 ±1	95 ±14	161 ±26	30 ±1	15 ±1
Mn ($\mu g\ g^{-1}$)	47 ±11	74 ±14	67 ±7	67 ±5	113 ±6	163 ±24	81 ±3	80 ±10
pH	4.36 ±0.01	4.29 ±0.03	4.27 ±0.01	4.41 ±0.04	4.17 ±0.02	5.45 -	4.31 ±0.01	4.25 ±0.05
Organic content (%)	6.07 ±1.24	4.93 ±0.43	3.42 ±0.14	2.72 ±0.36	13.87 ±1.01	5.45 ±0.47	2.47 ±0.13	4.05 ±0.24

sites were richest in K and the crest was richest in Na. There was little difference between sites in terms of pH, although C2 was approximately 1.3 pH units more basic than the other sites.

8.3.3.2 Lichen mineral element content.

Although lichen samples were collected monthly, mineral element content of the lichens was only analysed for the first five months (April to August inclusive). This was due to the extremely variable nature of the data, with large within-site variation at each collection. Variances were also heteroscedastic and it was unlikely that any reliable statistical analyses would have been possible. The data from the first five months of the sampling were pooled and means and error values obtained. These are presented in Figure 8.11 for K, Na, Ca and Mg and in Table 8.4 for Fe and Zn. The detailed monthly results are presented in Appendix C. Estimation of the thallus concentrations of Cu and Mn were abandoned after the first trials because of extremely low values which would have required the digestion of much larger samples to obtain reasonable results. Larger samples would aslo have been required for reliable analysis of thallus Al content because of the low sensitivity of atomic absorption spectroscopy to Al, and therefore these determinations were also abandoned.

From Figure 8.11 it is obvious that *Usnea* was significantly richer in Ca than *Umbilicaria* but there were no other obvious differences between the species in terms of mineral content. There were no real differences in the K content of the species and little pattern with site, although at some sites *Umbilicaria* had a higher K content than *Usnea*. The Mg content was stable across both site and species, while thallus Na content was variable in both species although somewhat more so in *Umbilicaria*. The pattern with site was not consistent between the species with *Umbilicaria* having high Na content at NM2 and C1, while the Na content of *Usnea* at these sites was not. The thallus contents of Fe and Zn were very variable and there was no definite trend with site (Table 8.4).

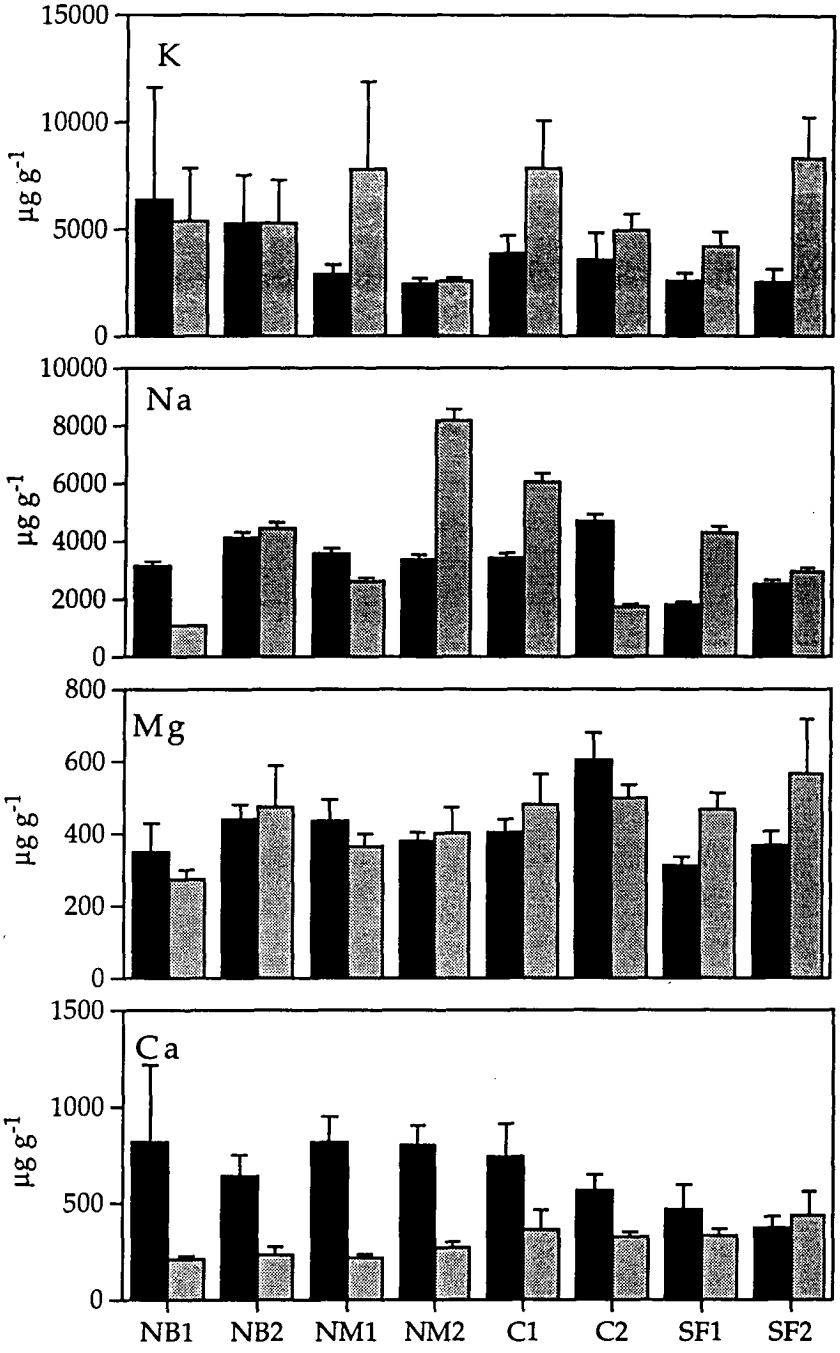

Figure 8.11 Mineral element content of *Usnea sphacelata* (solid bars) and *Umbilicaria decussata* (stippled bars). Vertical lines are one standard error.

TABLE 8.4 *Thallus concentration of Fe and Zn in ($\mu g\ g^{-1}$) ± one standard error for* Usnea *and* Umbilicaria

	Usnea		*Umbilicaria*	
Site	Fe	Zn	Fe	Zn
NB1	621 ±137	23 ±5	466 ±63	23 ±3
NB2	604 ±68	46 ±22	1293 ±477	42 ±6
NM1	684 ±145	22 ±5	939 ±122	22 ±3
NM2	794 ±118	17 ±3	1061 ±149	33 ±5
C1	269 ±79	21 ±3	884 ±224	76 ±40
C2	1048 ±122	88 ±45	995 ±111	40 ±4
SF1	1131 ±323	22 ±3	1157 ±147	40 ±4
SF2	797 ±133	22 ±4	1200 ±189	128 ±84

8.3.3.3 Lichen P content.

Lichen total P content was calculated for both species at each site for the first four months, after which instrument problems, coupled with some sample losses, prevented further P analyses. The thallus P content of *Umbilicaria decussata* and *Usnea sphacelata* are shown in Table 8.5 and the results of the analyses of variance are given in Table 8.6.

TABLE 8.5 *Lichen thallus P contents ($\mu g\ g^{-1}$) ± one standard error.*

Site	Species	April	May	June	July
NB1	*Usnea*	430 ±139	639 ±21	661 ±65	436 ±8
NB2	*Usnea*	335 ±67	508 ±76	428 ±51	417 ±59
NM1	*Usnea*	538 ±153	784 ±16	516 ±55	904 ±86
NM2	*Usnea*	915 ±258	343 ±32	468 ±22	405 ±60
C1	*Usnea*	1343 ±178	323 ±107	689 ±48	643 ±85
C2	*Usnea*	1395 ±441	569 ±2	561 ±70	565 ±17
SF1	*Usnea*	1247 ±305	643 ±113	309 ±112	780 ±10
SF2	*Usnea*	1348 ±415	470 ±204	636 ±121	367 ±65
NB1	*Umbilicaria*	397 ±45	- -	367 ±33	403 ±10
NB2	*Umbilicaria*	408 ±40	- -	675 ±38	455 ±124
NM1	*Umbilicaria*	538 ±153	784 ±16	516 ±55	904 ±86
NM2	*Umbilicaria*	1477 ±71	613 ±50	634 ±18	482 ±50
C1	*Umbilicaria*	1802 ±626	1059 ±148	1159 ±97	1105 ±53
C2	*Umbilicaria*	972 ±314	1041 ±74	899 ±7	1000 ±167
SF1	*Umbilicaria*	1598 ±66	903 ±18	890 ±130	1132 ±124
SF2	*Umbilicaria*	1384 ±384	825 ±28	824 ±89	1003 ±100

TABLE 8.6 *Results of the analysis of variance of natural log transformed P data (μg g^{-1}). The species x month interaction was not significant at p>0.05.*

Source	df	F ratio	p
Species	1	98.82	0.0001
Site	7	19.95	0.0001
Species x Site	7	10.63	0.0001
Month	3	23.30	0.0001
Species x Month	3	0.91	ns
Site x Month	21	7.18	0.0001
Species x Site x Month	19	2.29	0.005
Residual	124		

The significant interaction terms in the analysis of variance of the P data shows that the differences which occurred between months are both species and site specific. This can be seen from Table 8.5, where over a period of a month the mean P content in a particular species increased at some sites and decreased at others. The trend at a particular site was also dependent upon species. This can be seen at C2 where the P content of *Usnea* was highest in April and not significantly different in the other months, whereas the P content of *Umbilicaria* didn't alter significantly over the four months.

Despite these interactions, the main effects of species, site and month were highly significant (Table 8.6). Comparisons of means using the Ryan-Einot-Gabriel-Welsch test showed that *Umbilicaria* had a significantly higher P content than *Usnea* (927±53 and 608±29 μg g^{-1} respectively), the thallus P content was significantly higher in April (1051±58 μg g^{-1}) than in the other months which were all similar (May 657±30 μg g^{-1}, June 668±32 μg g^{-1}, July 661±22 μg g^{-1}). The thallus P content as a function of site fell into three groups, with lichens from the crest and south-face sites having the highest P content and the north-base sites having the lowest, with those sites in the middle being intermediate (Table 8.7).

8.3.3.4 Thallus N content

Total thallus nitrogen contents for both species at each site for the 12 months following April 1992 are given in Figures 8.12 and 8.13.
The analysis of variance for total thallus nitrogen showed that each of the main effects of site, month and species, had highly significant effects on

TABLE 8.7 *Mean P ($\mu g\ g^{-1}$) for each site (combined species and month) with the number of samples. Those means with the same letter are not significantly different at p=0.05.*

Site	no. samples	Mean P
NB1	45	218[a]
NB2	45	220[a]
NM1	48	331[b]
NM2	48	356[b]
C1	48	522[c]
C2	48	424[c]
SF1	48	480[c]
SF2	48	431[bc]

the nitrogen content of lichens, as did interactions of these terms (Table 8.8). Thallus N was significantly higher in *Umbilicaria decussata* (0.772%±0.012) than in *Usnea sphacelata* (0.717%±0.012) and higher in lichens from the crest region than in those from other sites (Table 8.9). The mean N content changed according to month (Figure 8.14). In general the lichen N content gradually increased over the year, but this was offset by the sudden decreases which occurred between June and July, as well as between October and December. The largest decrease occurred in November.

The monthly changes in N content of each species at each site (Figs 8.12 and 8.13) were more variable than in the pooled data (Figure 8.14), but they did reflect the major patterns. There was a large change in N content of both species during June at almost all sites, although the change differed in direction according to species and site. The most consistent change was that which occurred during the early summer, when N content of both species fell at most sites (Figure 8.12 and 8.13), although the exact timing differed according to species and site. The decrease was more pronounced in October for four species-site combinations (*Umbilicaria* at NM1, C2 and SF2, *Usnea* at C1), in November for six (*Umbilicaria* at NB1 and NM2, *Usnea* at NB1, NM1, NM2 and SF2) and in December for both species at SF1. For three species-site combinations (*Umbilicaria* at C1 and *Usnea* at NB2 and C2) the drop in N was more or less evenly spread throughout the early summer,

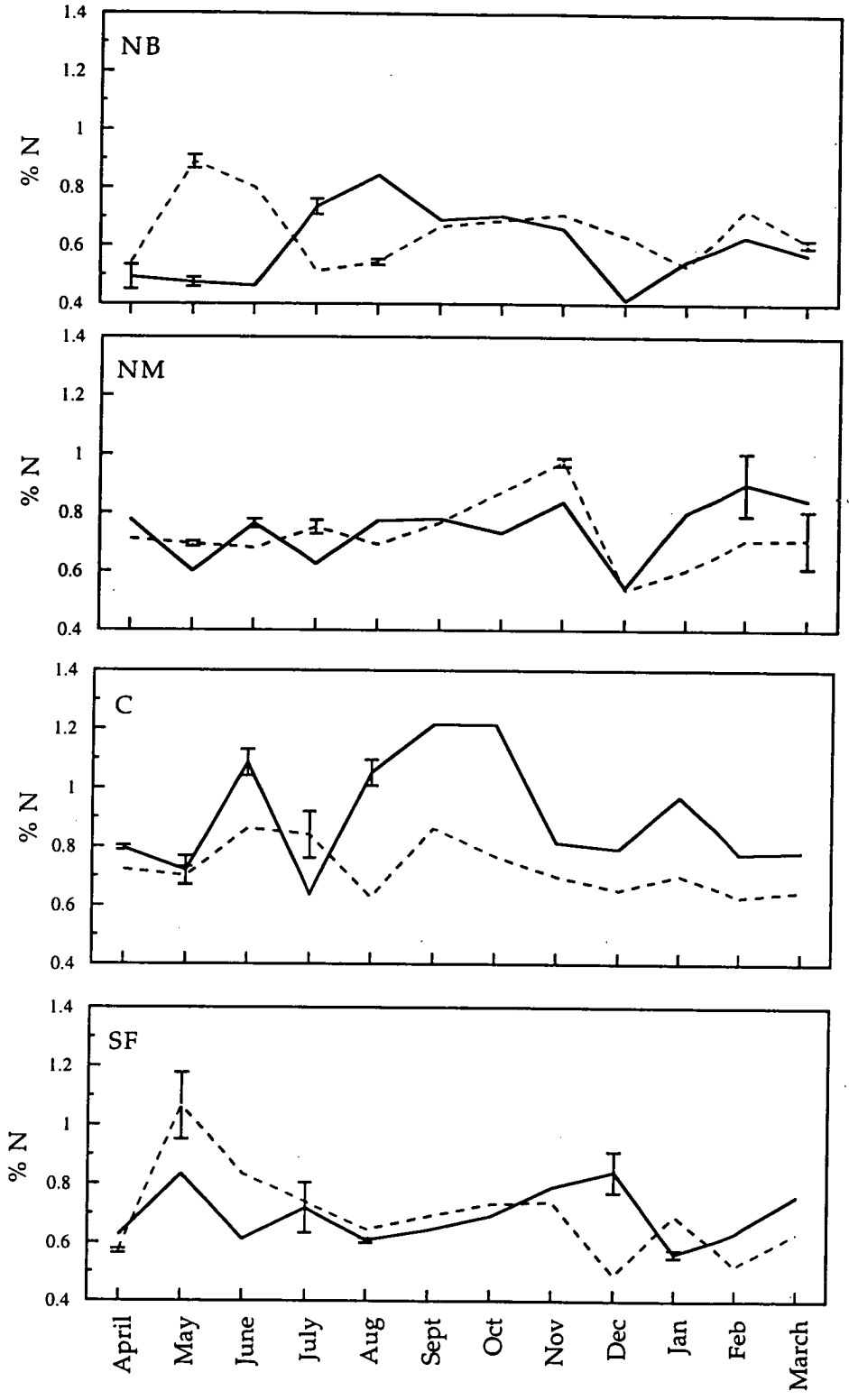

Figure 8.12 *Usnea sphacelata* N content. Vertical lines are ±standard error. Dashed lines indicate the second site in each location (e.g. NB2), while the first site is indicated by the solid line (e.g. NB1).

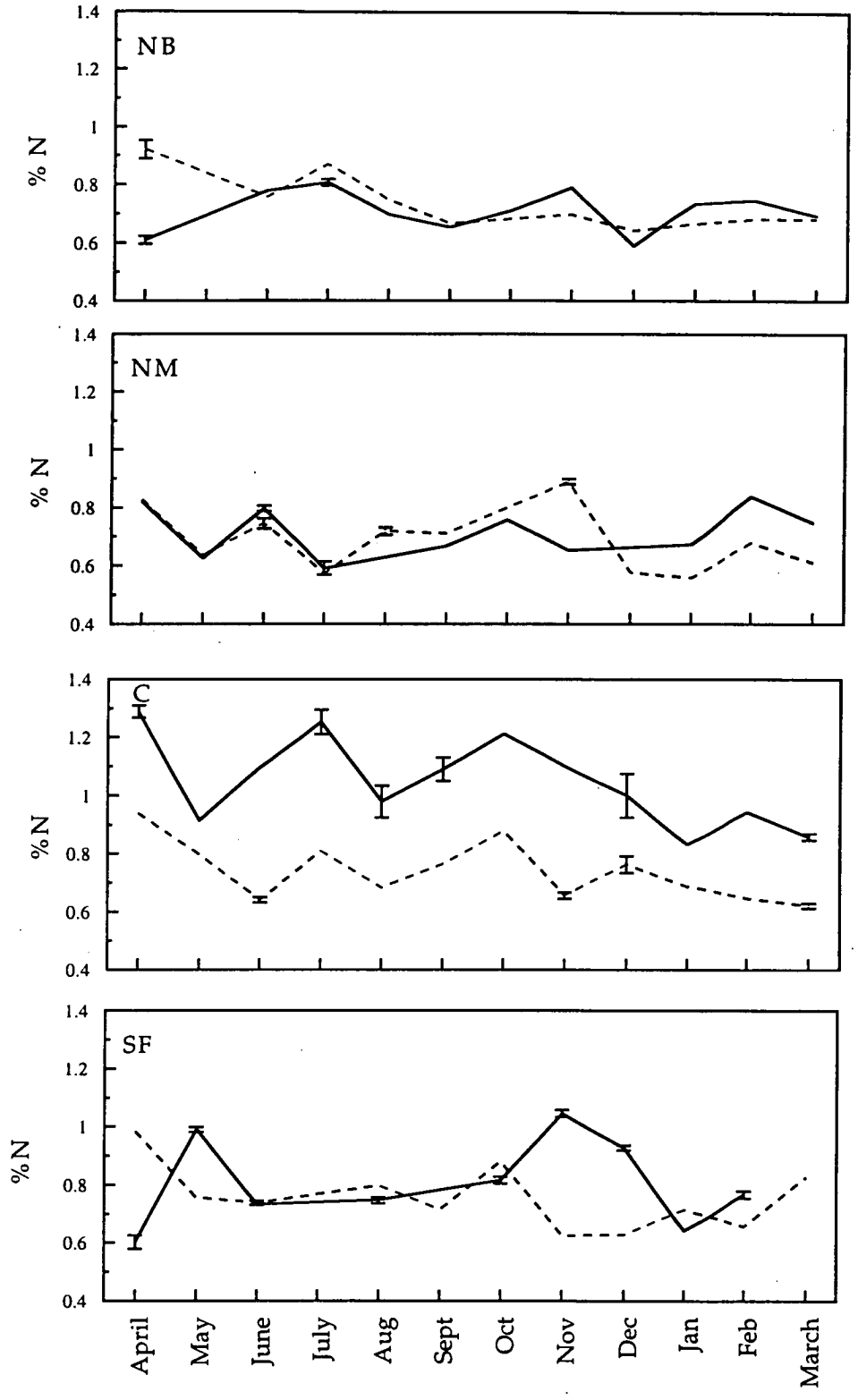

Figure 8.13 *Umbilicaria decussata* N content. Vertical lines are ±standard error. Dashed lines indicate the second site in each location (e.g. NB2), while the first site is indicated by the solid line (e.g. NB1).

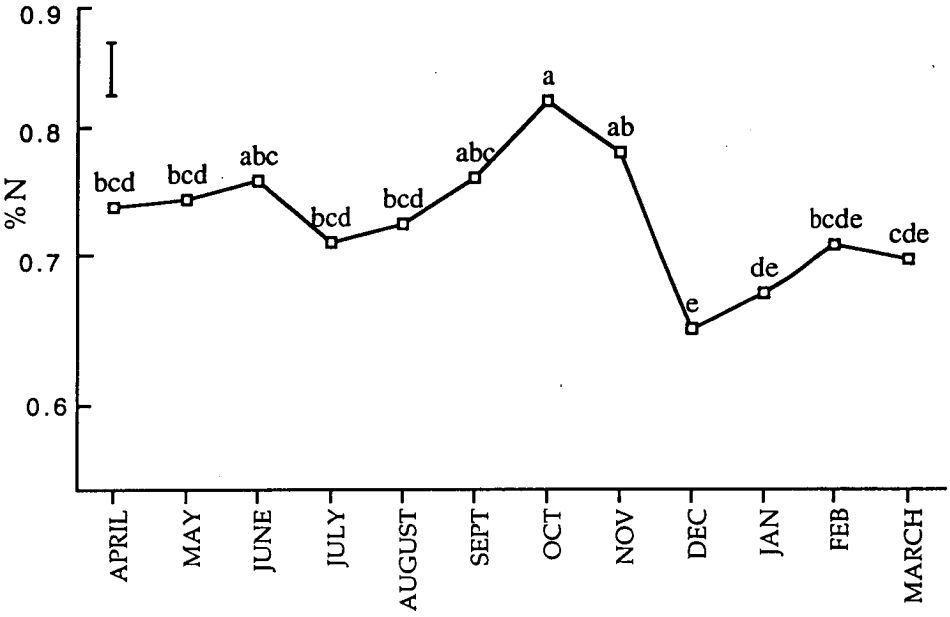

Figure 8.14 Mean monthly thallus N content. The vertical line is one standard error. Points with the same letter are not significantly different at p=0.05.

TABLE 8.8 *Results of the analysis of variance for natural log transformed %N data.*

Source	df	F ratio	p
Species	1	36.63	0.0001
Site	7	38.29	0.0001
Month	11	7.01	0.0001
Species x Site	7	5.75	0.0001
Species x Month	11	3.34	0.0003
Site x Month	74	4.02	0.0001
Species x Site x Month	70	1.83	0.0007
Residual	180		

TABLE 8.9 *Mean %N for each site (combined species and month) with the number of samples. Those means with the same letter are not significantly different at p=0.05.*

Site	no. samples	Mean %N
NB1	46	0.654^{c}
NB2	42	0.690^{bc}
NM1	48	0.726^{b}
NM2	44	0.698^{bc}
C1	48	0.960^{a}
C2	46	0.738^{b}
SF1	44	0.743^{b}
SF2	44	0.724^{b}

while there was no real change in the N content of *Umbilicaria* from NB2 over the summer period.

8.3.3.4 Interrelations between substratum and lichen thallus nutrition.

In general there was little correlation between the levels of mineral elements in the lichen thalli and those of the substratum (see Tables 8.3 and 8.4 and Figs. 8.9, 8.10 and 8.11). Thallus K and Na contents were independent of the substratum levels and the thalli were generally higher in both elements than the substratum on which they were growing. Thallus Mg and Ca concentration were also independent of the substratum levels, but the levels in the substratum were much higher than those in the lichen thalli. Neither Zn nor Fe levels in thalli were related to substratum levels. Thallus Fe content was always much lower than substratum levels. Thallus Zn contents varied by a factor of only

about six, while the substratum levels varied over a greater range, with the result that Zn levels in the substratum were higher than in thalli at Zn-rich sites, but lower than thalli in the relatively Zn-poor sites (Tables 8.3 and 8.4).

In contrast, both nitrogen and phosphate showed a definite relationship between thallus and substratum levels (Figure 8.15 and 8.16). Thallus N was linearly correlated with substratum total N (r^2=0.845, $p<0.01$), while no correlation was possible for the P data because of the extreme range of the substratum levels. It is clear, however, that the thallus P content rises linearly with substratum P up to a certain level, at which time it seems to plateau (Figure 8.16). Analysis of the relation excluding those samples from C1 and C2 showed that there was a significant correlation between the two variables over the initial, linear part of the response (r^2=0.888, $p<0.01$).

8.3.4 Discussion

There have been several studies on the interrelations of lichen mineral content, substratum nutrient content and local inputs, such as from sea spray and power stations (e.g. Puckett and Finegan 1980, Sloof and Wolterbeek 1993, Brown *et al.* 1994). These studies variously ascribe the major source of nutrients as dry-deposition, wet-deposition and substratum (Richardson 1995), and there is a common assumption (discussed in Brown *et al.* 1994) that lichens accumulate any locally abundant element, which is important in their use as biomonitors for pollution studies. Brown *et al.* (1994) dispute this assumption and describe the case of *Xanthoria parietina* in which thallus concentrations of Ca and Mg are largely independent of local conditions. This is undoubtedly the case here where the mineral content of the two dominant lichens is largely unrelated to their substratum. Most detailed analyses of the mineral interactions of lichens and their substratum deal with epiphytic lichens and are from the northern hemisphere (e.g. de Bruin and Hackenitz 1986, Gough *et al.* 1988, Sloof and Wolterbeek 1993) so comparisons must be cautious. However, the values presented here are generally similar to those reported in other studies, although differences do appear when the data are examined in detail. Levels of most mineral elements in *Usnea sphacelata* and *Umbilicaria decussata* were significantly different to other lichens from other places. In particular the thallus levels of K measured here were higher than those reported by Puckett and Finegan (1980), Garty *et al.* (1985) and Gough *et al.*

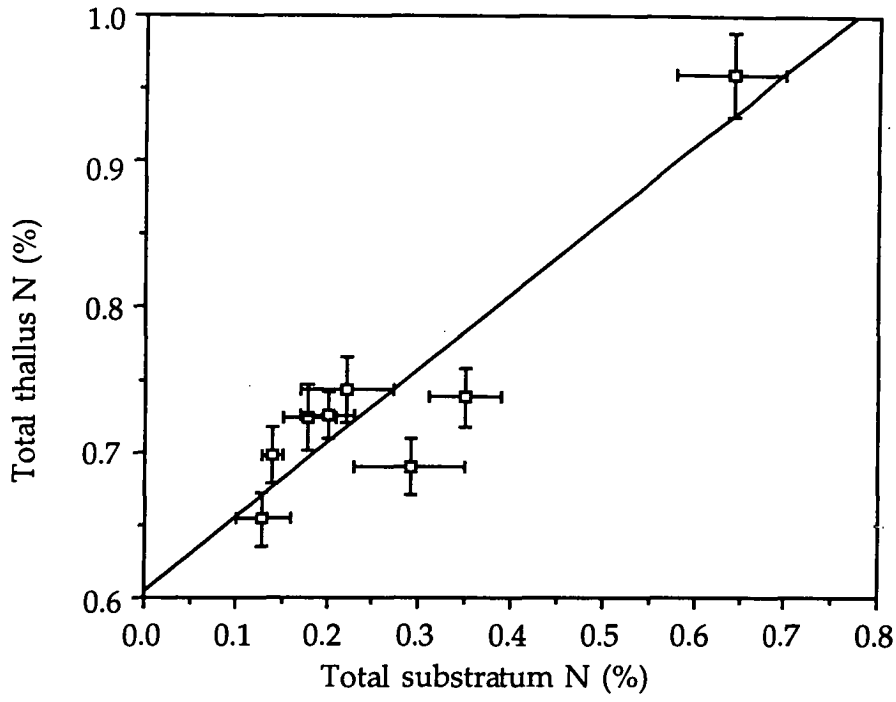

Figure 8.15 The relationship between susbtratum and thallus nitrogen contents in *Usnea sphacelata* and *Umbilicaria decussata*. Points are means for each site with ± one standard error in both directions. The diagonal line shows the slope of the linear regression.

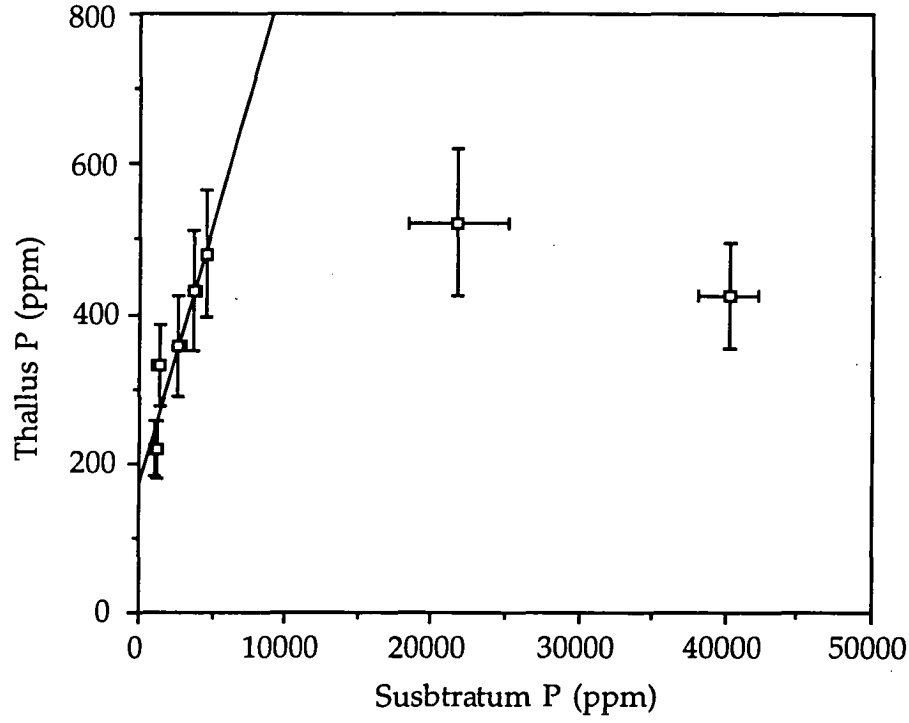

Figure 8.16 The relationship between thallus and susbtratum P levels. Points are the mean for *Usnea sphacelata* and *Umbilicaria decussata* thalli from each site ± one standard error in both directions. The diagonal line indicates the slope of the linear regression excluding the C1 and C2 values.

(1988), but quite similar to those of de Bruin and Hackenitz (1986). The Ca content of *Umbilicaria* and *Usnea* was much lower than any other published value for lichens. Zinc and Fe levels were similar to other published values for lichens, except where those lichens came from sites enriched with heavy metals (e.g. Sloof and Wolterbeek 1993).

In contrast to these differences, Smith's (1990) investigations of mineral content of *Usnea sphacelata* from Clark and Bailey peninsulas gave Mg, Fe, Ca and K values very similar to those found here. Smith's (1990) single record of *Usnea* Na content was somewhat lower than reported here, but his site of collection is believed to be further from the sea (pers. obs.). It is possible that the high concentrations of K and Na in the lichen thalli are an adaptation to the extreme climate of continental Antarctica, but this is not certain. Smith (1990) also reported a similar value for thallus P to those found here and a slightly lower N content. Thallus P levels were also similar in other studies (Garty *et al.* 1985, Gough *et al.* 1988).

Lichens mostly survive on substrata low in accessible N and P. Crittenden *et al.* (1994) discussed the problems with studies of lichen N and P nutrition and drew attention to the dearth of literature discussing lichen nutrition, with the exception of nitrogen-fixation. No continental Antarctic lichens are known to contain cyanobacteria as the photobiont, and so they are incapable of fixing atmospheric N_2. There have been few studies which analysed the effects on lichens of increased nutrition without concurrently raising the available water, thereby confounding the experiment. Longton (1988) reported that nutrients were unlikely to be limiting to the growth of lichens in maritime Antarctica, and Smith (1979) and Farrar (1976) argued similarly for lichens in general. Crittenden *et al.* (1994), however, stated that this has not been shown conclusively and believe that the growth of mat-forming lichens is curtailed by N and P limitation. This hypothesis was supported by experimental growth studies of lichen mycobionts in culture, which showed that growth ceased when the N content of the fungi fell below a certain point.

The changes in lichen N content can be explained in terms of their metabolic activity. Greenfield (1992) demonstrated that lichens in maritime Antarctica can retain sufficient N from precipitation to allow an annual biomass increment of some 7%, given no other limitations. In

the Windmill Islands, this input of N is mostly in the form of snow which falls year-round but more heavily in the winter months. Lichens are therefore likely to gradually accumulate N throughout the year. If growth was constant throughout the year, and exactly matched the input of N, the N content of lichens would remain constant. Growth of Antarctic lichens, however, is known to be strongly seasonal (see Ch. 5 and Ch. 6). Therefore the lichen N content increases when growth is slight or non-existent, such as in mid-summer and winter, and falls when lichen growth occurs at a rate greater than that of N accumulation, such as during the early summer, when snow melt and microclimatic conditions are conducive to lichen growth. This pattern is site-dependent since microclimatic conditions and snow accumulation are site-dependent. This is supported by the fact that those lichens from the site with the greatest accumulation of snow and therefore the latest onset of summer temperatures (SF1) had the latest drop in N content. It is also possible that there is some leakage of N from the thalli during periods of water uptake, such as during the early summer, and therefore it is possible that not all of the recorded decrease in thallus %N is due to growth.

The changes which occurred in thallus N content between June and July are puzzling in that they do not vary consistently with either species or site. Leakage of N from lichens is known to occur (Crittenden 1983), although most previous work has dealt with N-inputs from N_2-fixing lichens. Millbank (1978) showed that while N-leakage was minimal for *Lobaria pulmonaria* during rainfall, flooding caused significant loss of N from thalli. Therefore, it is possible that leakage of N occurred when lichens were flooded during the rewetting event in mid-June, which would explain the decrease in N content. In the cases where the N content increased, the situation is more difficult to explain. Since the thallus temperatures and water availability during the rewetting event would have allowed significant respiration to take place, there could have been a significant loss of carbon. Antarctic lichens also contain a significant concentration of soluble sugars which may be used as osmoticum (Melick and Seppelt 1994b), and these may be expected to leach out of the thallus during rewetting events. Together, these may have reduced the C:N ratio and consequently increased the relative N content on a dry weight basis. It might be supposed that leakage of N was unlikely since there was no great loss of K (see Section 8.2), however Crittenden (1983) has shown that it is possible for there to be significant

leakage of N from thalli at the same time as a net uptake of K. This can be explained by the cation exchange nature of the lichen, since K^+ and NH_4^+ would be trapped by binding sites on the cell wall, while organic N compounds, which formed the bulk of the leached N in Crittenden's (1983) studies, could leach freely. Therefore it is possible to postulate that the N content fell in cases where there was leakage of N greater than the loss of C due to respiration and leakage of soluble sugars, and an increase in N content where the loss of C was greater than N leakage, although this is not proven. The variable nature of the results might also indicate that there was a variable degree of flooding.

The decrease in thallus N which occurred during June is approximately equal to the difference between the mean thallus N content in April 1992 and that in March 1993. It is possible that the N content would have been more or less equal at the beginning and end of the sample period, had the rewetting event in June not occurred. If this were the case, then it is possible that lichens are growing at a rate which is equivalent to their uptake of N, and therefore are potentially limited by N availability. Crittenden (pers. comm.) has shown that over summer in the Windmill Islands, *Usnea sphacelata* thalli captured 91% of the nitrate and 87% of the ammonium in snow melt water. Together, this would indicate that either the lichens lose any excess N, which may occur at times such as during the early summer melt, or that their growth is curtailed by N limitation.

This study presents evidence that the substratum levels of N and P influence the nutritional status of the lichens growing on them. It may be argued that some of this influence is due to the presence of particulate matter in the extracellular space of the lichen thalli, but were this the case, we might also expect a correlation between other elements, particularly Ca which is so variable among sites. This is not the case, and since loss upon ignition is usually greater than 98% for these lichens (pers. obs. and D. Melick, pers. comm.), contamination by the substratum is slight. If we assume that the atmospheric deposition of elements is similar among the sites, then there is also the possibility that differences in lichen growth rates among the sites may cause the observed differences. There is some support for this hypothesis given the more severe microclimatic conditions prevailing in the crest regions, which are the sites of the highest thallus N and P concentrations, and hence the lower potential for growth at these sites. This may contribute to the

pattern, but even when the data for the crest region are ignored the correlation between substratum nutrient levels and those in lichen thalli are highly significant. Therefore, it is most likely that both *Umbilicaria decussata* and *Usnea sphacelata* take up both P and N from their substratum to an extent which is dependent upon the concentration of these elements in the substratum.

Thalli are enriched in both Na and K. Since no information is available on the atmospheric input of these elements it is not possible to define the dependence of the lichens on the substratum for these elements. Smith (1990) found that *Usnea sphacelata* thalli were enriched in K, and furthermore, that K concentration in soil under this species was lower in the top 1.5 cm than in the 1.5 cm beneath, which implies that K uptake from the substratum is possible, or that it is leached.

Future work should concentrate on the nutrient input from the atmosphere and the absorption of elements from meltwater by lichens. There is no information on the uptake of N and P from the substratum by any lichen species, since it is generally assumed that these elements are obtained by lichens almost exclusively by atmospheric deposition. Studies of N and P uptake may well clarify this issue.

Seasonal differences in the nutritional status of Antarctic lichens have not been demonstrated previously. This study shows that not only do changes occur, but they can be related to observed and hypothesised patterns of physiological activity.

Chapter 9

Ecophysiology of lichens in continental Antarctica.

9.1 General Conclusions.

The terrestrial ecosystems of Antarctica provide excellent systems for ecophysiological study, because the environmental determinants are so strong and Antarctic plants are relatively simple, with the macroscopic vegetation being dominated by lichens. The cold is bitter, the levels of photosynthetically active radiation are negligible for several months during winter and during summer the sun may shine for 24 hours a day. Continental Antarctica is also very dry and particularly windy. Most Antarctic soils are skeletal and low in nutrients. The lichen-dominated systems found in the northern Windmill Islands are simple enough that we have some hope of determining the environmental factors which control ecological processes, yet sufficiently complex to generate interesting models which may eventually prove applicable to less extreme regions. This study, by combining investigations of laboratory and field physiology with ecology and microclimatic estimation, has attempted to elucidate the factors which govern the distribution and abundance of the lichens which dominate the terrestrial vegetation of the Windmill Islands.

It is likely that the microclimate in the lichen habitat restricts the growth and survival of species. Lichens, and other terrestrial plants, resist continual frosting and thawing during summer so large amounts of osmoticum are probably required to prevent extensive tissue damage. Since there is a large amount of leakage of soluble carbohydrates from lichens subject to repeated freeze-thaw cycles (Melick and Seppelt 1992, 1994a), growth rates would be inversely related to the frequency of freeze-thaw cycles. The frequency of freeze-thaw activity is related to snow-lie, with those sites of latest-lying snow being exposed to the fewest freeze-thaw cycles (Ch. 3). The restriction of some species, such as *Umbilicaria aprina*, to sites of late-lying snow could reflect an inability to cope with repeated freeze-thaw cycles. It is possible that low temperatures in themselves are not as stressful as repeated cycles of freezing and thawing.

A blanketing cover of snow is known to confer protection against large swings in temperatures as well as attenuating very high light conditions (Kappen 1993, Ch. 3). The microclimatic conditions experienced by lichens during the winter were much less severe when those lichens were covered by a thick blanket of snow. Those lichens growing at SF1, NM1 and both NB sites were subjected to far fewer periods of very low thallus temperature. Thallus temperatures at SF1 were remarkably constant when compared to those at the nearby, but very exposed, C2 site. Not only are the lowest thallus temperatures avoided altogether, but so are the very large diurnal excursions which occur very early in the summer when the ambient temperatures are low and the incident radiation high (Ch. 3). This is the time of the most severe freeze-thaw activity and could well be a time of great stress to some lichen species.

While snow accumulation did significantly reduce the frequency of freeze-thaw cycles at the study site, sites of latest-lying snow had low numbers of species and low cover values, with some areas being devoid of lichen growth (Ch. 7). In these cases the protection from stressful climatic events afforded by a cover of snow must be outweighed by shortened periods of useful light and increased levels of thallus moisture during the summer melt. While the higher levels of water availability may be beneficial to an extent, there is obviously a point for each species where the cover of snow becomes a liability. Some species seem adapted to the moister conditions under snow banks, with species such as *Pseudephebe minuscula* and *Usnea antarctica* growing at high cover values low on the slope, while other species, such as the otherwise dominant *Usnea sphacelata*, are entirely excluded from these sites (Ch. 7). *Pseudephebe minuscula* has a higher photosynthetic activity at high thallus water contents in the field than the other two species studied (Ch. 5). This may explain its dominance in sites of late-lying snow. The field measurements show that, even for *Pseudephebe minuscula*, photosynthesis is prevented by extremely high thallus water content. Further studies of the environment under the snow are required to describe the likely activities of various lichens.

Although summer is the only period of temperatures suitable to normal plant growth, lichens in the Windmill Islands were photosynthetically inactive for the majority of the summer (Ch. 5).

Photosynthetic activity and growth are restricted to a very short period during early summer and perhaps again, although to a lesser extent, at the end of summer (Ch. 8). Measurements of photosynthetic activity during mid- to late-summer showed that all of the major macrolichen species were inactive except when moistened directly by snowfall or run-off (Ch. 5).

Models of the uptake of water from the atmosphere showed that once the major snow melt finishes, there is little to no uptake of water and hence very little metabolic activity (Ch. 6). The time of greatest water uptake is during the melt in early summer when the large amount of free water in the environment raises the humidity in the lichen microhabitat to a level where metabolic activity is possible for much of the time. This would enhance the direct uptake of water from snow melt and run-off, and allow metabolic activity in exposed lichens away from these sources of direct moistening. Furthermore, because of the long daylength during summer, lichens would be able to photosynthesise during the bulk of the time when water uptake occurred. The models of water uptake clearly indicate the timing of photosynthetic activity and growth, which coincides almost exactly with the onset of summer thallus temperatures.

Water uptake from the atmosphere in exposed sites was concentrated almost exclusively in November (Ch. 6). At this time, thallus temperatures ranged from well below -5°C to well over 10°C nearly every day at all sites except those still covered by snow. Previous models (summarised in Kappen *et al.* 1995) have described the temperature relations of photosynthesis in polar lichens, and state that they are rarely photosynthetically active when their thallus temperatures are above about 10°C. The major species of lichen in the Windmill Islands were photosynthetically active at temperatures above this, although it is not known whether their net carbon assimilation was negative or positive. If respiratory activity was great at these times, there was probably a low to negative carbon balance, despite the photosynthetic activity of the photobionts. The relationships between temperature and carbon acquisition are important and it is likely that during early summer, which is the time of nearly all of the photosynthesis and growth, there will be large ranges of assimilation rates during the day as the thallus temperature and water content and PPFD change. Earlier studies investigating

lichens under a thin cover of snow (Kappen *et al.* 1991) have shown such diurnal patterns and have modelled carbon assimilation over these periods. Further models are required for those lichens exposed to the atmosphere. New technology, which logs the presence of metabolic activity (Schroeter *et al.* 1991), should yield much information on the overall timing of photosynthetic activity in lichens from a range of microhabitats. Such information will provide crucial insights into the performance and surivival of various species of lichen in different microhabitats, thereby improving our understanding of the physiological determinants of lichen distribution.

Seasonal changes in the thallus concentration of nitrogen provide information on the uptake of nutrients as well as on temporal patterns of lichen growth. Since the acquisition of ammonium ions by lichens is not dependent on metabolic activity, and there is approximately four times as much ammonium as there is nitrate in snow at Casey (Crittenden in print), the uptake rate of nitrogen should be more or less constant throughout the year. Deviations from the gradual increase in lichen thallus nitrogen, therefore, must be either due to losses from the thallus or growth. The thallus concentration of nitrogen at the beginning and end of the 12 month sampling period were not significantly different, although the concentration was slightly lower at the end of the period (Ch. 8). Lichens accumulated nitrogen gradually over the year, but the increases were slightly more rapid during the summer months of December to February. This may be due to changes in the deposition rates or to the increased level of nitrogen capture due to metabolism-dependent nitrate-uptake. Of most interest, however, are the decreases in thallus nitrogen which occurred between October and December, with the greatest decrease occurring during November. This corresponds with the maximum time of growth proposed by the models of water uptake. It is possible that there was some leaching of organic nitrogen from the thalli during this period, but the changes in %N are more likely to be due to growth which occurred at this time, thereby increasing the C:N ratio. The slight decrease which occurred in February may well be due to net growth as well, since some growth would be expected at the end of summer when the first substantial snowfalls occur.

The decrease in %N during June was due to the unusual rewetting event which allowed respiration and probably resulted in the loss of

organic nitrogen (Ch. 8). The rewetting event caused very few other changes in the elemental composition of the lichen thalli, and except for *Usnea sphacelata* from the crest region, did not significantly affect the lichen's membrane integrity (Ch. 8). It is therefore likely that most of the lichens were not significantly stressed by being warmed in the dark, flooded and rapidly refrozen when completely submerged. *Usnea sphacelata* from the crest sites also showed the greatest decrease in %N at this time which indicates that the leakage of organic nitrogen may have been correlated with the loss of membrane integrity. Overall, *Usnea sphacelata* was more stressed than *Umbilicaria decussata* during winter, as evidenced by the higher proportion of potassium located outside the cell in *Usnea sphacelata*. This corresponds with the greater capacity of *Umbilicaria decussata* to grow in the most exposed of sites (Ch. 7).

The slight overall decrease in thallus nitrogen content can probably be related to the losses of organic nitrogen which occurred during June. In a normal year without a significant rewetting event during the middle of winter, thallus nitrogen content would probably cycle around a constant value, with the annual growth requirements for nitrogen matching the yearly uptake rate.

Substratum nutrition has a definite effect on the distribution of minor species, mostly those which have previously been described as nitrophilous (Smith 1990, Ch. 7). However, the distribution of the dominant species was independent of variations in the availability of substratum nutrients, even though the range of some nutrients, particularly calcium and phosphate, was great (Ch. 7). The thallus concentrations of most of these elements was also unrelated to substratum nutrition (Ch. 8). The only nutrients in which the thallus concentration was dependent upon substratum were nitrogen and phosphate. It is unlikely that the observed patterns in these nutrients are due to differences in growth rates among the sites, since this would be expected to alter the concentration of all captured elements, none of which show any trend with site. The major species must absorb those elements required (N and P) from the substratum while excluding others, such as calcium. The high concentration of K in the cells may be related to the high osmotic potentials required by lichens to survive freezing, but there is no evidence for or against this.

Since lichens usually grow in sites chronically deficient in available nitrogen, it is usually assumed that they are more or less dependent on atmospheric inputs of nitrogen. On Clark Peninsula there is a definite relationship between the total nitrogen content of two of the major species and that of the substratum on which they are growing, which indicates that there is a possibility of nitrogen uptake from the substratum. If this were the case, then we might expect lichens from sites of higher available nitrogen content to grow more quickly than those from more nitrogen-deficient sites, given similar water availability. This would result in a greater lichen biomass in nitrogen-rich sites.

While the sites investigated here present a range of substratum nitrogen levels (Ch. 7 and Ch. 8), they also present a range of microclimates and water availability (Ch. 3). The crest region, which is highest in terms of substratum nitrogen, is also the coldest and most exposed and has the lowest levels of snow accumulation. Therefore lichens at the crest sites would be most limited by water availability. If the atmospheric inputs of nitrogen were similar among sites, it is possible that the trend in water availability contributes to the relationship between thallus and substratum nitrogen levels. However, lichens from the SF1 site, which has relatively high water availability, have a high nitrogen content. Therefore, it is likely that lichens are obtaining some of their nitrogen from the substratum.

Most ecological and physiological studies of Antarctic lichens propose that low temperatures, and hence water availability, are the prime limiting factors for growth and survival. While this is true, there is evidence that the growth of Antarctic lichens may also be limited by nitrogen nutrition (Ch. 8). These two factors are not mutually exclusive since, while the primary limitation is undoubtedly water availability, the growth of lichens during the times of available water could be limited by their demand for N and the amount of stored N. The situation may be similar in terms of P, but this is not known. Kappen *et al.* (1995) proposed a model of growth and carbon assimilation by polar lichens which integrates all of the known controls and feed-backs. I propose that the effects of nitrogen availability on growth be added to this model, since it is possible that during times in which no other known factors are limiting, nitrogen demand and the amount of stored nitrogen may control a lichen's

maximum growth rate. Field experiments during November, the time of maximum lichen growth, in which the available amount of nitrogen is altered and the photosynthesis and growth of lichens is monitored, may help to determine the controls on lichen growth of available nitrogen. A long-term experimental manipulation of lichen nitrogen nutrition, coupled with growth studies, would yield even more conclusive results.

Individual thalli of *Usnea sphacelata* and *Umbilicaria decussata* appear thicker and heavier than those from the north-mid and north-bottom sites, but there are no measurements of lichen biomass. Estimates of lichen growth rates and biomass from several sites with a variety of substratum nitrogen levels are required to determine the contribution of substratum nitrogen to lichen growth. It is possible that the extreme microclimatic conditions at the crest region severely limit lichen growth, and that survival in this site is entirely dependent upon one or two months of rapid photosynthesis and growth. If, as hypothesised above, nitrogen is a limiting factor when microclimatic conditions are conducive to growth, the availability of nitrogen would be crucial in these environments. If this is the case, the high levels of substratum nitrogen, and the consequently high concentrations of N in the thallus, may allow growth at a more rapid rate in early summer than at those sites with lower nitrogen availability. Similarly exposed sites with low nitrogen contents should be investigated to determine if this is the case.

This rationale would predict that the areas of greatest lichen growth will be sheltered sites with high availability of nitrogen. At the study knoll on Clark Peninsula, the greatest cover values, which should approximately indicate biomass, occurred in sites such as these, which were close to the crest (and therefore high in N) yet provided with reasonable cover. These sites are all dominated by *Usnea sphacelata* which, as the macrolichen with the largest aerial thallus, provides most of the biomass. A similar relationship between biomass and substratum nutrition has been reported from maritime Antarctica (Gremmen *et al.* 1995), and should be quantitatively determined for a continental Antarctic site.

In conclusion, the patterns of distribution and abundance in lichen species at a continental Antarctic site can be at least partially explained

in terms of the microclimatic conditions, substratum nutrition and patterns in the species' water relations and photosynthetic activity. The time of lichen growth is related to exposure and duration of snow lie. Growth was found to be limited to a few months of the year, nearly all of which occur at the onset of summer. High levels of substratum nutrition restrict the occurrence of several minor species but do not affect the distribution of major species. Those species which are more tolerant of high thallus water content are also more tolerant of late-lying snow, although very late-lying snow excludes all species. Further work is required to elucidate some features of the growth and survival of the dominant life form in the terrestrial vegetation of continental Antarctica.

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Appendix A

Results of the TWINSPAN analysis of species occurrence data. Cover scores are as in Figure 7.2. Top two lines give the quadrat numbers when read in columns from top to bottom. The bottom four lines are the sociation scores.

Sociation		1	4	2	5	3	6
		667777777777888556644562	212266	1111122461145	2 1122333345	234445 33333455	466
Quadrat number		890123456789012674679577	6937825	24678901811552	470225012824	38939016345634567401	303
	SPECIES						
3	Usnea antarctica	2222222222222223233--31	-------	--1222122-1123	322-1-22--2-	-3333333343-33333454	---
26	Pleopsidium chlorophanum	----------	--1----	----------	----------	----------	---
19	Rhizocarpon flavum	----------1-----1	-------	---------1-1-1	----------	----------	---
5	Pseudephebe minuscula	44444444444444444554444	-11--11	33-1-122332222	-32232133332	22323334422222235434	---
4	Umbilicaria decussata	222222222222222-22-2333	2443313	33333433333333	423333433223	22323223132233334423	---
25	Physcia caesia	----------	----1--	-1--1-----1---	-1----------	--1----------11-----	---
23	Xanthoria mawsonii1	----------	21-----	-1----------	1--1-1------	----------	---
16	Lecidea cancriformis	----------111-11--	1111111	1111111-111111	111-11111111	1-111-111111-111-1-1	1--
7	Buellia frigida	----------1-	21---11	----------2113	1112-2-2-1--	------11--11--------	---
24	Xanthoria mawsonii2	----------	11-----	-1----------	2--2--------	----------	---
12	Rhizoplaca melanophthalma	----------1111111	-11-111	-1111111111---	11111211111-	111-11-111-111-11111	1--
6	Buellia soredians	----------1----11	--1----	31122132--11--	11-13--11-11	123231---33411213231	---
2	Usnea sphacelata	----------221-	11111-1	332111222-2222	41232-222-22	333442332244534322334	---
17	Lecidea sp.	----------11	---1-1-	--------1-----	-1-1-11--1--	----21-1-1--121--12-	221
13	Candelariella flava	----------1-------	-------	1---1---112--2	-21--2--213-	222221213221---2-222	---
11	Buellia latemarginata	----------	-------	-1---1--------	1---1-1-1---	-1--2----------2-2-	---
18	Lepraria	----------	-------	----------	---1-----1--	----2-1------1---1--	---
15	Lecanora expectans	----------	-------	----------	--11---1---1	11-111-11---1-1-----	---
14	Rinodina olivaceobrunnea	----------1-	-------	----------	---1----21-1	2332333322--121-1222	---
9	Buellia papillata	----------1-	-------	----------1---	--11---111-1	-1111-11-11-11-111-1	---
29	Moribind moss	----------1-	-----1-	11------1-----	234322233332	33324333322-23222223	--2
27	Grimmia antarctici	----------	-------	----------	2--1-1------	---1----------	---
21	Caloplaca athallina	----------	-------	----------	---1--------	----------	---
20	Caloplaca citrina	----------	-------	----------	------21----	----------112-1---	---
10	Buellia lignoides	----------	-----1-	----------	----11----1-	--21-2----------1--	2--
8	Buellia grimmiae	----------	-------	----------2-	-1322--22212	1-11333----------	---
		00000000000000000000	0000000	00000000000000	111111111111	1111111111111111111	111
		00000000000000000000	1111111	11111111111111	000000000000	0000000000000000000	111
		00000000000000000001111	0000000	11111111111111	000000000000	1111111111111111111	
		0000000000000001111	0011111	00000000001111	011111111111	0000000011111111111	

APPENDIX B

Concentrations of cations at various locations in the thallus during June and July. Sites are described in the text.

					Na				K				Mg				Ca			
Site	Sp.	Rep	Month	Wt (g)	Extra-	Wall	Intra-	TOTAL	Extra-	Wall	Intra-	TOTAL	Extra	Wall	Intra-	TOTAL	Extra-	Wall	Intra-	TOTAL
Blank					7	6	0	**13**	2	2	41	**44**	0	0	0	**1**	1	1	1	**3**
NM	Usnea	a	June	0.107	149	137	210	**496**	179	469	2453	**3102**	1	65	197	**263**	0	66	332	**398**
NM		b	June	0.102	108	161	2485	**2755**	138	889	2124	**3151**	1	89	228	**319**	0	93	710	**802**
NM		c	June	0.122	82	56	1239	**1377**	126	167	4891	**5185**	8	92	275	**374**	0	82	141	**223**
NM	Umb	a	June	0.104	229	294	463	**986**	131	73	2326	**2530**	25	64	194	**283**	5	80	49	**134**
NM		b	June	0.102	332	693	801	**1826**	159	162	5784	**6106**	33	114	428	**575**	8	106	44	**158**
NM		c	June	0.110	271	505	765	**1541**	231	87	3750	**4068**	15	79	721	**815**	3	67	72	**143**
NM	Usnea	a	July	0.118	77	35	692	**803**	191	674	4849	**5715**	1	49	274	**324**	3	41	603	**647**
NM		b	July	0.112	215	485	240	**940**	442	233	8721	**9396**	0	159	225	**384**	0	106	117	**222**
NM		c	July	0.121	34	647	344	**1025**	97	225	3800	**4122**	1	109	245	**355**	0	65	455	**520**
NM	Umb	a	July	0.109	70	160	531	**760**	65	111	5167	**5343**	10	88	169	**267**	1	96	42	**139**
NM		b	July	0.107	256	57	709	**1021**	68	66	5222	**5355**	14	100	180	**294**	1	111	35	**147**
NM		c	July	0.115	164	212	1262	**1638**	70	88	3227	**3385**	8	70	181	**258**	1	79	38	**118**
SF	Usnea	a	June	0.107	100	682	565	**1347**	53	123	4820	**4996**	7	114	200	**321**	0	72	51	**123**
SF		b	June	0.111	56	269	1395	**1720**	59	125	7374	**7559**	0	83	249	**332**	0	48	38	**86**
SF		c	June	0.111	69	148	311	**527**	162	95	6055	**6311**	0	89	195	**284**	0	65	38	**103**
SF	Umb	a	June	0.101	308	82	429	**819**	145	90	8099	**8334**	2	97	381	**480**	0	98	24	**121**
SF		b	June	0.102	342	327	410	**1080**	149	113	2004	**2266**	6	90	351	**447**	0	89	32	**122**
SF		c	June	0.099	156	166	462	**785**	115	112	4820	**5047**	2	89	279	**369**	3	88	22	**113**
SF	Usnea	a	July	0.120	66	376	615	**1057**	154	313	8265	**8732**	0	128	142	**270**	0	120	29	**149**
SF		b	July	0.109	170	209	551	**931**	109	378	4694	**5182**	0	79	181	**260**	0	69	42	**111**
SF		c	July	0.131	82	228	325	**636**	146	338	7000	**7484**	4	81	166	**251**	2	68	43	**113**
SF	Umb	a	July	0.106	203	96	548	**847**	367	219	7474	**8060**	20	67	287	**375**	21	78	26	**126**
SF		b	July	0.113	195	177	553	**925**	115	170	3937	**4221**	0	58	321	**379**	0	65	80	**145**
SF		c	July	0.105	181	142	295	**618**	234	267	8310	**8811**	0	68	271	**339**	0	80	30	**110**

APPENDIX B (cont.)

Concentrations of cations at various locations in the thallus during June and July. Sites are described in the text.

					Na				K				Mg				Ca			
Site	Sp.	Rep	Month	Wt (g)	Extra-	Wall	Intra-	TOTAL	Extra-	Wall	Intra-	TOTAL	Extra	Wall	Intra-	TOTAL	Extra-	Wall	Intra-	TOTAL
C	Usnea	a	June	0.116	285	169	805	**1259**	62	93	7300	**7454**	24	121	766	**911**	4	99	546	**648**
C		b	June	0.109	255	305	299	**859**	60	125	3287	**3472**	18	259	289	**565**	4	184	270	**458**
C		c	June	0.114	394	166	566	**1126**	110	100	4875	**5084**	32	119	286	**436**	9	74	93	**176**
C	Umb	a	June	0.107	211	23	356	**590**	92	54	1250	**1396**	27	107	160	**295**	16	148	42	**205**
C		b	June	0.105	375	67	248	**690**	170	52	8089	**8312**	17	89	317	**423**	14	141	73	**229**
C		c	June	0.104	376	58	414	**848**	132	62	6744	**6938**	23	104	238	**365**	36	122	55	**213**
C	Usnea	a	July	0.103	98	96	205	**399**	228	113	1055	**1396**	5	92	233	**330**	6	64	46	**116**
C		b	July	0.119	126	93	1028	**1247**	76	95	2083	**2254**	16	54	384	**453**	4	26	1547	**1577**
C		c	July	0.126	150	94	982	**1226**	118	85	2176	**2378**	16	68	110	**194**	6	37	1572	**1614**
C	Umb	a	July	0.127	301	99	392	**792**	213	145	5800	**6158**	23	107	942	**1072**	13	137	100	**249**
C		b	July	0.132	188	82	1315	**1585**	189	192	25966	**26346**	16	79	593	**688**	8	107	45	**160**
C		c	July	0.108	422	102	664	**1188**	165	73	16014	**16252**	16	100	753	**870**	7	125	72	**204**

APPENDIX C

Mineral content of *Umbilicaria decussata* and *Usnea sphacealata* thalli between April and August 1992 at the 8 sites at the study knoll on Clark Peninsula. Figures in bold face are the means for each month, species, site and element. Figures in normal face are one standard error. All values are in $\mu g\ g^{-1}$.

Month	Site	Species	K		Na		Ca		Mg		Fe		Zn	
4/92	NB1	*Umbilicaria*												
5/92	NB1	*Umbilicaria*												
6/92	NB1	*Umbilicaria*	**814**				**254**	74	**216**	37	**612**	237	**43**	2
7/92	NB1	*Umbilicaria*	**4032**	1621	**4866**	3385	**204**	27	**186**	37	**425**	107	**23**	7
8/92	NB1a	*Umbilicaria*	**3363**	716	**1164**	98	**196**	7	**388**	22	**618**	124	**37**	4
8/92	NB1b	*Umbilicaria*	**10297**	8277	**1104**	191	**215**	44	**281**	27	**257**	27	**30**	3
4/92	NB2	*Umbilicaria*	**1821**	0	**395**	0	**490**	0	**1292**	0	**5004**	0	**26**	0
5/92	NB2	*Umbilicaria*												
6/92	NB2	*Umbilicaria*	**15505**	1442	**1201**	200	**296**	5	**546**	60	**1256**	158	**63**	6
7/92	NB2	*Umbilicaria*	**3148**	1017	**5285**	3914	**211**	50	**235**	74	**681**	192	**51**	5
8/92	NB2	*Umbilicaria*	**2654**	49	**7106**	4558	**129**	15	**394**	56	**694**	148	**25**	3
4/92	NM1	*Umbilicaria*	**38971**	0	**788**	0	**224**	0	**390**	0	**700**	0	**16**	0
5/92	NM1	*Umbilicaria*	**2522**	647	**866**	85	**273**	34	**350**	98	**1020**	187	**29**	10
6/92	NM1	*Umbilicaria*	**11021**		**1567**		**237**	25	**452**	40	**1217**	101	**28**	4
7/92	NM1	*Umbilicaria*	**5455**	2302	**1236**	37	**192**	21	**319**	78	**985**	366	**18**	5
8/92	NM1	*Umbilicaria*	**2159**	394	**16874**		**151**	32	**316**	83	**451**	224	**13**	6
4/92	NM2	*Umbilicaria*					**318**	62	**458**	18	**1696**	128	**32**	2
5/92	NM2	*Umbilicaria*	**3074**	17	**15245**	1991	**425**	98	**170**	10	**1096**	111	**28**	3
6/92	NM2	*Umbilicaria*	**2129**	217	**3176**	994	**187**	21	**776**	234	**1414**	418	**60**	14
7/92	NM2	*Umbilicaria*	**2482**	249	**7737**	5810	**241**	44	**254**	89	**545**	156	**27**	1
8/92	NM2	*Umbilicaria*	**2379**	321	**4698**	2567	**172**	33	**352**	55	**556**	148	**16**	2

APPENDIX C (cont.)

Month	Site	Species	K		Na		Ca		Mg		Fe		Zn	
4/92	C1	*Umbilicaria*	**0**	0	**0**	0	**299**	0	**364**	0	**182**	0	**17**	0
5/92	C1	*Umbilicaria*	**4416**	1549	**8645**	4032	**276**	51	**198**	45	**528**	170	**34**	3
6/92	C1	*Umbilicaria*	**11117**	2527	**4639**	2666	**650**	397	**623**	185	**692**	240	**220**	148
7/92	C1	*Umbilicaria*	**16252**	10094	**1188**	396	**204**	44	**870**	202	**2380**	421	**31**	4
8/92	C1	*Umbilicaria*	**2404**	199	**8115**	3372	**292**	52	**398**	51	**669**	150	**24**	4
4/92	C2	*Umbilicaria*	**2096**		**779**		**349**	169	**467**	176	**666**	191	**31**	0
5/92	C2	*Umbilicaria*	**8143**		**1418**		**243**	32	**488**	38	**1161**	155	**48**	2
6/92	C2	*Umbilicaria*	**6978**	262	**2079**	65	**330**	25	**514**	109	**969**	267	**51.2**	6
7/92	C2	*Umbilicaria*	**4098**	161	**1461**	102	**349**	22	**388**	43	**532**	76	**34**	7
8/92	C2	*Umbilicaria*	**3617**	438	**2269**	943	**329**	29	**525**	76	**1318**	111	**23**	0
4/92	SF1	*Umbilicaria*					**427**	21	**572**	42	**1499**	157	**26**	2
5/92	SF1	*Umbilicaria*	**3393**	676	**8220**	6547	**448**	24	**300**	104	**1265**	156	**42**	3
6/92	SF1	*Umbilicaria*	**2105**		**1561**		**226**	38	**546**	100	**776**	373	**58**	2
7/92	SF1	*Umbilicaria*	**5663**	943	**1254**	49	**224**	24	**447**	36	**1088**	383	**34**	4
4/92	SF2	*Umbilicaria*	**6580**	3874	**1484**	866	**277**	32	**574**	85	**1338**	280	**47**	13
5/92	SF2	*Umbilicaria*	**3626**	385	**7787**	5973	**308**	57	**449**	283	**1858**	497	**27**	0
6/92	SF2	*Umbilicaria*	**12595**	2460	**3027**	1842	**700**	468	**859**	549	**820**	258	**354**	306
7/92	SF2	*Umbilicaria*	**8975**	5364	**1058**	174	**419**	6	**343**	82	**1002**	428	**52**	12

APPENDIX C (cont.)

Month	Site	Species	K		Na		Ca		Mg		Fe		Zn	
4/92	NB1	*Usnea*					186	6	309	5	796	38	14	1
5/92	NB1	*Usnea*	4664	1866	7504	5304	318	88	213	81	1099	220	25	4
6/92	NB1	*Usnea*	5400	1681	794	90	212	21	319	15	640	47	42	5
7/92	NB1	*Usnea*	3370	592	4008	3056	646	186	575	214	453	37	25	2
8/92	NB1a	*Usnea*	10726	8995	729	176	1093	449	317	18	366	69	15	2
8/92	NB1b	*Usnea*	7877	4821	5197	3834	2473	237	359	13	374	11	16	3
4/92	NB2	*Usnea*												
5/92	NB2	*Usnea*	1592	255	867	444	545	293	342	4	859	45	14	5
6/92	NB2	*Usnea*	5990	4188	6773	4021	347	18	510	138	565	100	44	5
7/92	NB2	*Usnea*	2840	147	1398	376	1111	216	514	104	324	20	126	92
8/92	NB2	*Usnea*	10477	8496	7699	2057	495	54	367	12	530	70	10	1
4/92	NM1	*Usnea*	1162		444		1190	51	417	90	1012	297	11	4
5/92	NM1	*Usnea*	2920	816	5421	4367	850	285	419	127	650	447	14	4
6/92	NM1	*Usnea*	1934	83	5537	2568	707	416	349	22	501	60	14	1
7/92	NM1	*Usnea*	2621	684	1009	88	462	155	342	15	407	89	48	9
8/92	NM1	*Usnea*	3181	80	6405	1919	1087	381	744	282	1095	688	15	1
4/92	NM2	*Usnea*					561	42	460	13	1532	60	18	2
5/92	NM2	*Usnea*	1628	525	4902	3630	585	180	320	79	496	102	12	3
6/92	NM2	*Usnea*	2646	743	4192	2471	1024	269	367	33	514	83	34	6
7/92	NM2	*Usnea*	2874	430	1158	409	876	266	308	35	492	89	14	1
8/92	NM2	*Usnea*	2389	329	6005	3403	962	304	441	38	938	216	8	3

APPENDIX C (cont.)

Month	Site	Species	K		Na		Ca		Mg		Fe		Zn	
4/92	C1	*Usnea*					746	394	524	214	723	481	16	3
5/92	C1	*Usnea*	1686	130	6843	1440	499	115	256	8	181	15	20	2
6/92	C1	*Usnea*	6580	1819	1358	95	428	89	412	23	192	20	40	4
7/92	C1	*Usnea*	4072	1817	3849	2612	1113	482	332	75	181	19	12	4
8/92	C1	*Usnea*	2427	194	2015	461	1112	620	462	33	199	47	10	1
4/92	C2	*Usnea*												
5/92	C2	*Usnea*	2884	663	9608	4312	513	16	528	91	1231	190	61	2
6/92	C2	*Usnea*	1726		1418		843	257	4	264	643	96	225	152
7/92	C2	*Usnea*	13156		1299	224	414	60	626	138	1119	430	27	8
8/92	C2	*Usnea*	2822	141	3094	1145	445	66	588	110	1221	225	18	1
4/92	SF1	*Usnea*					230	66	336	56	1026	188	8	6
5/92	SF1	*Usnea*	1755		3049	1971	352	71	269	18	1040	513	18	2
6/92	SF1	*Usnea*	2748		1793		634	400	290	79	1799	1127	37	2
7/92	SF1	*Usnea*	2780	584	974	156	578	315	356	37	626	72	21	2
4/92	SF2	*Usnea*	1552	43	344	53	428	34	395	15	732	17	19	2
5/92	SF2	*Usnea*	239	88	7983	6121	316	115	326	90	990	226	14	3
6/92	SF2	*Usnea*	5084	311	1005	30	525	167	430.6	135	762	429	39	6
7/92	SF2	*Usnea*	2937	155	1334	339	199	28	305	46	768	331	16	3

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EXPOSURE AND NUTRIENTS AS DELIMITERS OF LICHEN COMMUNITIES IN CONTINENTAL ANTARCTICA

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Abstract: Lichens dominate the terrestrial vegetation of the ice-free regions of continental Antarctica. Vegetation patterns were studied in the Windmill Islands Oasis, Wilkes Land, continental Antarctica, in relation to edaphic features to elucidate the factors that govern lichen distribution and abundance. Vegetation was studied on a low rounded knoll on Clark Peninsula some 3 km North East of the present Casey station. Substratum nutrient levels vary considerably across the knoll due to the presence of an abandoned penguin rookery on the crest and the uneven topography provides both sheltered and exposed sites. Along a 130 m-long transect crossing the knoll from South to North, a total of 25 species of lichen and one moss were identified, the vegetation being dominated by *Umbilicaria decussata, Pseudephebe minuscula, Usnea sphacelata* and *U. antarctica*. TWINSPAN analysis of species distributions identified six sociations, the distribution of which were related to substratum structure and chemistry. Several species were restricted to nutrient-rich zones while late-lying snow restricted all species to varying degrees.

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Uptake of Water from the Atmosphere by Lichens in Continental Antarctica

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Abstract

Microclimate relative humidity and temperature and lichen thallus temperature were measured from August 1992 to January 1993 at the crest of a hill on Clark Peninsula in the Windmill Islands, continental Antarctica. The water potential of the air in the lichen microhabitat was modelled and compared with the water potential assumed to be necessary for lichen photosynthesis due to water vapour uptake. It was found that for most of the spring the atmospheric water potential was too low for water vapour uptake by exposed lichen. In all there were only 351 h during which water vapour uptake could have occurred, most of this falling in November. The results indicate that water vapour uptake by exposed lichen will occur during the period of snow melt at the beginning of summer, but only rarely at other times.

Keywords: Antarctica, lichen, photosynthesis, water vapour uptake, water potential, microclimate

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Field photosynthetic activity of lichens in the Windmill Islands oasis, Wilkes Land, continental Antarctica

M. J. Hovenden, A. E. Jackson and R. D. Seppelt

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In order to ascertain whether the major species of continental antarctic macrolichens are photosynthetically active during summer conditions, the chlorophyll fluorescence of three lichen species [*Umbilicaria decussata* (Vill.) Zahlbr., *Pseudephebe minuscula* (Nyl. ex Arnold) Brodo and Hawksw. and *Usnea sphacelata* R. Br.] was monitored in the vicinity of Casey Station, Wilkes Land, continental Antarctica using a PAM-2000 modulated fluorescence system. Lichens were studied when in equilibrium with the atmosphere as well as when moistened by snow showers. Photochemical quantum yield was estimated as $\Delta F/F'_m$ and related to thallus water content as well as microclimatic conditions. Lichens were photosynthetically active only when moistened by snow fall or by run-off from snow melt. The levels of photosynthetic activity in the field for all species were influenced by microenvironmental conditions and patterns in response were site and species specific. Highest levels of photosynthetic efficiency occurred when thalli were at intermediate water contents. Photosynthetic activity was reduced by cold as well as warm, bright conditions. Highest thallus water contents occurred during the middle of the day after substantial falls of snow. *P. minuscula* maintained highest thallus water contents at all sites and appears to have a high water compensation point which is related to its observed distribution patterns. *Umbilicaria decussata* studied in the laboratory did not become photosynthetically active even when exposed to 95% relative humidity (RH) for 51 h and, when dehydrating after artificial wetting, showed an optimum thallus water content for photosynthesis of ca 90% dry weight and a thallus water compensation point of about 35% dry weight. In the field *U. decussata* did not become photosynthetically active except when moistened by snow. *Usnea sphacelata* exposed to the atmosphere had low thallus water contents (ca 30%) which was not related to RH. The results indicate that the lichens are photosynthetically inactive for most of the summer period and are totally reliant on snow as a water supply. This is important when modelling carbon gain and growth rates of continental antarctic lichens.

Key words – Antarctica, chlorophyll fluorescence, electron transport rate, lichen, photochemical quantum yield, *Pseudephebe minuscula*, *Umbilicaria decussata*, *Usnea sphacelata*, water content.

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Phytogeography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, Continental Antarctica

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Keywords: Biogeography, Cryptogam, Ecology, Moss, Plant dispersal

Abstract

The distribution and frequency of bryophyte and lichen vegetation on ice-free regions of the Windmill Islands are presented using data derived from aerial photography and ground surveying. The qualitative and quantitative plant cover of sites are listed and related to the topography and major soil characteristics of each site. The richest associations of macrolichens and bryophytes occurred on the metamorphic northern peninsulas. Species richness and frequency was generally reduced on the charnockitic southern peninsula and the islands which have been deglaciated longer. Salinity varied significantly throughout the region with the highest levels in the northern islands reflecting the presence of penguin colonies. In such sites bryophytes and lichens were virtually absent. Wind blown sea-spray contributed far less salts than direct excretion from penguins. On the peninsulas snow cover and site exposure appeared to delimit plant distribution. Higher salt levels from sea-spray on the northern aspects of the peninsulas seemed to have negligible impact on vegetation patterns with the possible exception of *Biatorella cerebriformis* which was encountered only inland. The total phosphorus and nitrogen levels of the skeletal soils were generally low except in eutrophic sites adjacent to penguin colonies. The vegetation patterns are discussed in terms of the climate, topography and species autecology.

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Utility of Modulated Fluorescence in Measuring Photosynthetic Activity of Antarctic Plants: Field and Laboratory Studies

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Abstract. Antarctic terrestrial plants face severe physiological stress conditions daily. In winter there is extreme cold and darkness. During summer there is continuous light for some months and plant surface temperatures may fluctuate through more than 50°C diurnally. Conditions are almost uniformly desiccative, except during spring when snow melt saturates thalli and plants may be completely inundated. The study of photosynthesis in these conditions is fundamental to a proper understanding of plant persistence, productivity and growth in polar regions. Lichens dominate the terrestrial vegetation of Antarctica and are therefore of great interest. Lichen photosynthesis has been shown to be dependent upon thallus water content and temperature as well as the irradiance incident on the thallus. Conventional infrared gas analysis (IRGA) techniques have been used most widely to study lichen photosynthesis in both the field and laboratory. Recent progress in the development of pulse amplitude modulated fluorescence systems has allowed the investigation of chlorophyll fluorescence in the field under naturally illuminated conditions. This paper highlights the utility of modulated fluorescence systems for the study of antarctic lichen photosynthesis, relates fluorescence results to those obtained by IRGA techniques, identifies problems inherent in fluorescence analysis of lichens and discusses possible areas of future research.

Extra keywords: Antarctica, chlorophyll fluorescence, electron transport rate, lichen, photochemical quantum yield, terrestrial plant, water content.